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ARBETEN FRÅN BOTANISKA INSTITUTIONERNA I UPPSALA
UTGIVNA AV PROF. E. MELIN OCH PROF. J. A. NANNFELDT

STUDIES IN THE NORTH-WEST EUROPEAN SPECIES OF RORIPPA s. str.

BY

BENGT JONSELL

UPPSALA 1968
A.-B. LUNDEQUISTSKA BOKHANDELN
(I DISTRIBUTION)

SYMBOLAE BOTANICAE UPSALIENSES

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PREFACE

This study was begun in the summer of 1960, when I, following a proposal by Dr O. Hedberg, decided to look closer at some interesting announcements about the pollen morphology and the chromosome numbers of some *Rorippa* species. The obscure hybrids growing at Lake Mälaren not far from Uppsala also offered an incitement. The work on these partial problems revealed further problems and showed the desirability of studying as much as possible of the variation met with and to elucidate its taxonomic significance. Mainly for practical reasons but also because of contemporaneous research on the genus in Czechoslovakia and the United States, the work has been restricted to the Nort-West European species.

To by far the greatest extent the investigations have been performed at the Institute of Systematic Botany, Uppsala. To Professor J. A. Nannfeldt, Director of this Institute, I convey my deep thanks for his continuous interest in my work, for many valuable suggestions and kind criticism, as well as for the facilities granted for my studies at the Institute.

To a high degree I am indebted to Dr O. Hedberg, who introduced me to the field of vascular plant taxonomy and who in numerous discussions has generously given me support and good advice during the progress of my work.

To Professor N. Hylander I tender my sincere thanks for valuable discussions, for much information especially concerning literature and terminology, and also for his help in supplying material through the seed-exchange of the Uppsala Botanical Garden.

Many persons have kindly contributed living plants from various parts of Europe and many have given valuable support in other respects. I will mention especially Professor E. Almquist, Drs Birgitta and Curt Forsberg, Dr Inga Hedberg, Dr N. Lundqvist, Mr I. Nordin, Dr O. Olsson, Professor B. Pettersson, Dr R. Santesson, and Dr T. Willén. To those and to many other friends and colleagues among botanists in Uppsala I express my cordial thanks.

Parts of my work have been carried out at other Nordic or at British Institutes. From those and from many other herbaria I have received loans and other information or material. I am much obliged to Directors, Curators and all other persons who have been engaged on my behalf. I am especially indebted to Mr D. Meikle, Kew, and Dr A. Melderis, British Museum (Nat. Hist.), who gave me much support during a two months' stay in London, and to Mr G. Aymonin, Paris, Mr M. Breistroffer, Grenoble, and Dr N. Tzvelev, Leningrad. My thanks are also

due to Mr H. W. Howard, Cambridge, and Mr G. A. Mulligan, Ottawa, who gave me opportunities to study the voucher specimens of their determinations of chromosome numbers in *Rorippa*, and to Dr R. L. Stuckey, Columbus, Ohio and Mr P. Tomšovic, Prague, for discussions and information.

A number of pollen preparations were made for me at the Palynological Laboratory, Stockholm-Solna, and for this I am much indebted to Professor G. Erdtman and Dr Siwert Nilsson. The latter made also valuable suggestions on palynological terminology.

For careful preparations of microscopical slides and for other technical assistance I am very grateful to Mrs Gunilla Blomstedt, Mr A. Olsson, and Mrs Ulla-Britt Ukkonen, as well as to members of the staff at the Uppsala Botanical Garden for supervision of the cultivated material. For the linguistic revision I am obliged to Mrs Carolyn Hörner, for the drawing of Figs. 6 and 21 to Mr J. Induss, and for the typing of the manuscript to Miss Aina Alm.

My investigations have been promoted by grants from the Swedish Natural Science Research Council, the Swedish Academy of Science (Hierta-Retzius fond för vetenskaplig forskning, Enanderska fonden), Uppsala University (Liljewalchs resestipendiefond, Lennanders fond, Anslaget för främjande av ograduerade forskare, Anslaget för fältarbeten) and from "Botaniska Sektionen av Naturvetenskapliga Studentsällskapet" in Uppsala. The National Research Council, Reykjavík, gave me permission for field research in Iceland. For all this support I express my sincere gratitude.

May I finally tender my warmest thanks to my wife, Dr Lena Jonsell, for her multifarious help and continuous encouragement during this work.

Institute of Systematic Botany, Uppsala. January 1968

Bengt Jonsell

I. INTRODUCTION

Survey of the genus

Like many other genera of the *Cruciferae Rorippa* has been circumscribed in various ways. In the wide sense taken by Schulz (1936) the genus was estimated to contain some 50 species, but a calculation today gives about 70 valid species. Many groups of the genus are, however, imperfectly known. Schulz (op. cit.), who used the generic name *Nasturtium*, discerned six sections, two of which contain European species. They are the large section *Rorippa* and the small section *Cardaminum*, to which Schulz attributed five species.

The type-section, *Rorippa*, has a wide circumpolar, Holarctic distribution, but does not contain any really Arctic taxa. As certainly indigenous the section extends southwards to Central America, Japan, Himalaya, the Near East, and the Mediterranean region, but it is probably not indigenous anywhere in Africa, as far as only taxa that clearly belong to the section are considered. The section would comprise c. 40 species, about one half of which are exclusively American, while the other half is confined to the Old World. Only one species, *Rorippa palustris* (L.) Bess. is widely distributed in the Holarctic area, and is over vast parts of eastern N. America, N. Europe, and Asia the only representative. Two more species, *R. islandica* (Oed. ex Murr.) Borb. and *R. barbareifolia* (DC.) Kitagawa are common to Eurasia and America, in the North Atlantic and in the Beringian areas respectively.

Some fairly clear species groups may be discerned within the section. One includes the well-known species *Rorippa amphibia* (L.) Bess. and *R. sylvestris* (L.) Bess. and is distributed with about eight species in Europe and W. Asia, especially the Pontic region. Some of these species have been introduced to America.

Very close to this group and sometimes hybridizing with members of it is a number of species, which I shall refer to as the *Rorippa islandica* group. It is distinguished through the tendency to annual life and to small flowers in connexion with autogamy, and is rich in species, especially in western North America. The group counts at least 16 species, only two of which occur in Europe, *R. islandica* and *R. palustris*. A number of species close to *R. palustris*, which have been described from tropical and subtropical regions have not been counted, since they might well be naturalized populations of *R. palustris* that have been regarded as new taxa.

Two other species groups stand probably rather isolated from the taxa mentioned. One is on the whole South European–Aegean, with the widest ranging species, *Rorippa pyrenaica* (Lam.) Rchb. reaching S. Germany and Central France. Two others, *R. lippizensis* (Wulfen) Rchb. and *R. thracica* (Griseb.) Fritsch, occur in the Balkan peninsula and one, *R. icarica* Rech. fil. is an Aegean endemic. The status of some of these taxa is, however, doubtful. They are perennial mountain plants without notably weedy tendencies, and are morphologically distinguished from *R. sylvestris* and allied species a. o. through the persisting leaf-rosette and the distinctly reticulate seed-coat (cf. Ch. 3). Boissier (1867) called this group "*Xerobia*"[1] in contrast to *R. palustris*, *R. sylvestris* and related taxa, which he called "*Heliobia*", thus stressing the ecological differences. He also included a species of the Near East, *Nasturtium macrocarpum* Boissier, which I have not studied at all, but which Schulz (1936) placed in another section. In the following I shall refer to these plants as the *R. pyrenaica* group.

The other group includes about six perennial, thick-leaved North American species, the best known being *R. sinuata* (Nutt.) A. S. Hitchc., and has by Stuckey (1965) been proposed to constitute a section of its own (*Sinuatae*).

In the section *Rorippa* Schulz (1936) included also a number of little known species, whose affinities to the groups mentioned are obscure, and for some of those the position in the genus is questionable. Among those are the East-Asiatic *Rorippa globosa* (Turcz.) Thellung, perhaps related to the *R. islandica* group, the South African *R. fluviatilis* (E. Mey. ex Sond.) R. A. Dyer, which Schulz (op. cit.) placed in sect. *Rorippa* and the N. American *R. aquatica* (Eaton) Palmer & Steyerm., which has a habit close to *R. amphibia*, but diverges a. o. in its white flowers. It is often placed in *Armoracia* or in a genus of its own, *Neobeckia*.

The section *Cardaminum*, as comprised by Schulz (1936), is distributed in both Eurasia, N. Africa and America, but the two well-known species, *Rorippa nasturtium-aquaticum* (L.) Hayek (the type-species) and *R. microphylla* (Boenn.) Hyl. are indigenous only in Eurasia. Many authors, particularly British ones, prefer giving generic rank to sect. *Cardaminum*, as the genus *Nasturtium*. The differences against the type-section comprise seed-coat structure, nectarial localization (cf. Ch. 3) and not least the habit, which points more to *Cardamine* than to the section *Rorippa*. No hybrids or taxa intermediate between these sections are known. Such features may warrant an independent position. Without much better knowledge of the genus a decision on this point is impossible, however, and I shall here maintain the section *Cardaminum*. For practical purposes I will, as in the title of this work, use "*Rorippa* s.str." to refer to the genus, sect. *Cardaminum* excluded.

The four remaining sections discerned by Schulz (1936) are completely extra-

[1] Boisser used the generic name *Nasturtium*. Borbás (1878), who employed *Rorippa* used the forms "*Xerobiae*" and "*Helobiae*".

European and occur mostly in tropical–subtropical regions. They would contain at least 20 species. All these sections are imperfectly known and both their rank and circumscription must be regarded as tentative.

Two small taxa, sometimes attributed to *Rorippa*, were by Schulz and also earlier regarded as separate genera. They are the Mediterranean genus *Sisymbrella* and the Andine *Kardamoglyphos*. At least for the former generic rank is generally accepted (Flora Europaea 1964).

Position in the family

The difficulties of obtaining more than a purely schematic system of the *Cruciferae* are well known. A thorough attempt to elaborate a natural system was made by Hayek (1911), who also gave a survey of all important systems raised before his time. After that the most weighty contributions have been given by Schulz (1936) and Janchen (1942). The latter criticized Schulz and accepted a modified version of Hayek's system. *Rorippa* was by all these authors placed in the tribe *Arabideae*, which, besides *Arabis*, consistently includes the well-known genera *Cardamine* and *Barbarea*. Hayek and Janchen, though emphasizing different characters, placed the two latter genera and *Rorippa* in the same subtribe, *Cardaminineae*, while *Arabis* was brought to another. From Schulz's arrangement no such affinity is evident, but his system is, as stressed by Janchen, on the whole rather schematic. Affinities of *Rorippa* to *Cochlearia*, usually placed in the tribe *Lepideae*, have also been suggested (Janchen 1942). Manton (1932) regarded *Cardaminineae* (s. Hayek) as a cytologically natural group.

Previous investigations

In spite of the size and wide distribution of the genus few studies devoted to *Rorippa* have been published. An exception is sect. *Cardaminum*, where the classical cytotaxonomic study by Howard & Manton (1946) resulted in the discovery of *R. microphylla*. This was followed by several papers treating various aspects of these plants in various regions (e.g. Howard 1947*a*, 1947*b*, Howard & Lyon 1950, Hylander 1950, Green 1955, 1962 and Jonsell 1963).

As to the section *Rorippa* fairly much has been written about the many forms in Central Europe where hybridization plays a prominent role (e.g. Tausch 1840, Borbás 1878, 1879*a*), but no modern treatment of this complex exists. In recent times some smaller groups of species have been discussed, e.g. the *R. pyrenaica* group (Turrill 1931), and some N. American taxa (Rollins 1961, Stuckey 1966*b*). The latter work is part of a largely unpublished thesis (Stuckey 1965) about the genus *Rorippa* in N. America. Rather much was earlier written about *R. palustris* in N. America (e.g. Butters & Abbe 1940, Fernald 1940). There are also, of course, a number of pure descriptions of new taxa, which are mostly peripheral to the

species treated here and therefore put aside. Observations about the genus are otherwise found in floras or in studies of morphological, cytological or other aspects. They will be referred to in the special chapters.

Aims and delimitation

From various points of view the need of further research in the sect. *Rorippa* has been emphasized. Among the problems observed are those of the European hybrids and of the *R. pyrenaica* group (Flora Europaea 1964), of the supposed differences between *R. palustris* in Europe and America (A. Löve 1954) and of the total Holarctic differentiation within this species (Hultén 1945), of the variation in *R. sylvestris* (Erdtman 1958, 1963*a*, 1963*b*) and in *R. amphibia* (Rechinger 1960). The taxonomic signification of the cytotypes and questions of indigenity and dispersal in cultivated regions are also matters worthy of investigations.

Not all of these questions will be treated here and some of them will be only partially discussed. The sect. *Cardaminum* is excluded since it has already been well investigated in Europe (cf. above). Since I wanted as much as possible to base the studies on living plants, in cultivation as well as in the field, I considered a limitation to the N.W. European species necessary. N.W. Europe means here the Nordic floristic area (Denmark and the Faeroes, Sweden, Norway, Finland, Russian Fennoscandia[1] and Iceland, cf. Hylander 1953) and the British Isles. I have not aimed, however, at a monographic treatment of the section within an exactly defined area, since that would have many impractical consequences. For many problems the studies were chiefly restricted to Scandinavia,[1] e.g. those of indigenity and dispersal, and of hybridization, where more than occasional experience of the situation in the field is desirable. The knowledge of the distribution of the cytotypes is also much greater for Scandinavia than for other parts of the area. On the other hand no taxonomic conclusions should be made without regarding the species over a wider range. For the *R. islandica* group, where the N.W. European situation suggested taxonomic changes, I have therefore extended the study to areas of special interest, viz. eastern N. America (incl. Greenland) and the Alps in particular. In the other species, for which I found no reasons to change the current circumscriptions, I only made preliminary observations of material outside N. W. Europe. I shall not express any opinion whether it would be justified in any other parts of the distributional range of the species treated to discern or include taxa. Nor have I decided upon the delimitation of these species against species in other parts of the world, though I shall briefly point to some problems about related taxa. To this end I will also report some chromosome numbers of

[1] *Scandinavia* = Denmark, Sweden, Norway and Finland. *Fennoscandia* = the Nordic floristic area except Denmark, the Faeroes and Iceland.

species not growing in N. W. Europe. Since my principal aim is to supply facts for a taxonomic revision I have left aside or only touched many questions that *per se* may warrant further studies.

Survey of species treated

In most floras three species of *Rorippa* s.str. are recognized as regular members of the N. W. European flora. They are nowadays usually called *Rorippa amphibia*, *R. sylvestris* and *R. islandica*. In this work I will divide the last-mentioned species into two, which will obtain the names *R. islandica* and *R. palustris*. The former has within N. W. Europe a restricted Atlantic range, while the latter is widely distributed. Thus four species are stabilized in the region, each of which is accorded a separate section of Ch. 6. A fifth species, *R. austriaca* (Cr.) Bess., is hardly more than an occasional alien. But a hybrid between it and *R. sylvestris* is nowadays constant in many urban areas. *R. austriaca* has therefore not been treated separately but is merely discussed in connexion with its hybrid. One more hybrid, *R. amphibia* × *sylvestris*, was found to be of importance in N. W. Europe, while two *R. palustris* hybrids, *R. amphibia* × *palustris* and *R. palustris* × *sylvestris* seem to arise only exceptionally. A Pontic species, *Rorippa brachycarpa* (C. A. Mey. in Ledeb.) Hayek has appeared as an occasional alien in easternmost Fennoscandia, viz. in Russian forts in Karelia olonetsensis (Fagerström 1944) and on railways in the Kirovsk region, Lapponia Imandrae (Flora Murmansk. obl. 1956). It will be touched on in p. 96.

The N. W. European species of *Rorippa* s.str. are primarily plants growing under moist conditions, in shallow water or on shores of lakes, streams and other freshwater bodies. An equally prominent feature is their sensitivity to competition, which implies that open soil, fresh or often disturbed, is a condition for their existence. Where the vegetation becomes definitely closed they disappear, and all the species are therefore to some extent ephemeral. Through their claim of open space they are highly favoured by cultivation and they even occur as true weeds, totally dependent on human activity at least over wide ranges of their areas. So they may come to grow in dry soil remote from water-bodies.

Material

The basic material has on the one hand been a stock of living plants, on the other herbarium material. Most of the living plants have been collected on field-trips to various parts of N. W. Europe. In Central and South Sweden I have collected through all the years 1960–1966. In N. Fennoscandia and in South and Central Finland I travelled chiefly in 1961, in parts of Norway also in 1962, 1963 and (to a small degree) in 1964, in Denmark 1962 and 1966, in Iceland 1962 and in the British Isles in 1964 and (to a small degree) in 1965. I have also collected a few plants in N. Germany, the Netherlands and Belgium. The samples comprised

if possible about five plants from each locality, but from populations of special interest, e.g. hybrid swarms, far larger samples were brought into cultivation. In most samples of *R. amphibia* and *R. sylvestris* only one clone is represented.

Through the seed-exchange of the Uppsala Botanical Garden I obtained a fairly large number of samples especially of *R. palustris*, and in some cases seeds from recent herbarium material gave rise to plants. The seeds germinated on filter paper kept moist under small plastic shades. 5–10 seedlings were kept from each seed sample. The total number of living samples of different species and hybrids of the sect. *Rorippa* is c. 450, mainly from N. W. Europe. About 50 are from the rest of Europe and c. 25 from N. America. Since the species often grow together the total number of localities represented is somewhat smaller, c. 400. All the samples are listed in App. 1. Each collection is given a reference number preceded by the letter J. Within a sample the various plants were marked a, b, c etc. In hybrid swarms, however, clearly different clones were given separate numbers.

All plants were transferred to pots and kept in moderate shade. Most of them were kept outdoors also in the winter. Seedlings and young plants were kept in a greenhouse, but were as soon as possible transferred to the open. Only especially susceptible material was constantly placed in the greenhouse. Voucher specimens of all the cultivated material will be preserved in UPS.

The living plants were used for determinations of chromosome numbers, observations of phenotypic *v.* genotypic variation, development from seeds, duration, fertility etc., and for crossing and isolation experiments. They also complemented the herbarium studies of morphological variation, especially in attempts to correlate features possible to study only in living plants with the variation observable in the herbaria.

The cultivation has not allowed free expansion of the perennial species, and for *R. amphibia* it has even implied a rather unnatural habitat. Therefore not only ecological but also morphological observations in the field were necessary, especially concerning formation of shoots and runners.

The herbarium material was either received on loan or studied on visits. The following enumeration gives the scope of material investigated in each herbarium. The names of the herbaria are abbreviated according to Lanjouw & Stafleu (1964). An asterisk points out the herbaria I have visited.

AAU (Danish *R. austriaca, R. sylvestris* and their hybrids), BG (Norwegian *Rorippa*), BM* (all *Rorippa*), BP (type of *R. austriaca*), BR (Belgian *R. amphibia*), C* (all *Rorippa*), CGE* (all *Rorippa*), CHUR (*R. islandica* and *R. palustris* from the Alps), DAO (Canadian *R. palustris*), DBN (Irish *R. islandica* and *R. palustris*), DUL (*R. palustris*), E* (all *Rorippa*), G (*R. islandica* and *R. palustris* from the Alps, types), GB* (Nordic *Rorippa*), GH, A, NEBC (part of N. American and E. Asiatic *R. palustris*), H* (all *Rorippa*), IB (*R. islandica* and *R. palustris* from the Alps), ICEL* (Icelandic *Rorippa*), L (Netherlandic *R. sylvestris*), LD* (all *Rorippa*), LE (selected sheets of *R. islandica* and *R. palustris* from U.S.S.R.), LINN*, MIN (one type), NMW* (all *Rorippa*), O*

(Nordic *Rorippa*), OXF* (all *Rorippa*), P (parts of French *R. amphibia*, *R. islandica* and *R. palustris*), PRC (types), S* (all *Rorippa*), SLBI* (British *Rorippa*), TL (*R. islandica* and *R. palustris* from the Pyrenees), TRH* (Norwegian *Rorippa*), TROM (*R. palustris* from N. Norway), TUR* (all *Rorippa*), TURA* (all *Rorippa*), UPS* (all *Rorippa*), UPSV* (all *Rorippa*), W (Austrian *R. amphibia; R. islandica* and *R. palustris* from the Alp-region), ZT (Swiss *R. amphibia*, *R. islandica* and *R. palustris*).

The herbarium material constituted the basis for studies of morphological variation and of distributions. For the areas outside N. W. Europe it was practically the sole source. The various characters observed and measured are discussed in Ch. 3, the variation itself in Ch. 6. Much of the variation is visualized in scatter diagrams (cf. Anderson 1949, O. Hedberg 1957). Since the diagrams are based on mean values of the measurements in each specimen or collection it is necessary for the reliability that not too strong an intra-individual variation amplitude is hidden. The approximate sizes of these amplitudes in various organs are given in Ch. 3.

Distribution maps were drawn only in a few special cases (Figs. 7, 13). Otherwise the works by Hultén (1950) and Perring & Walters (1962), both based on most information available, almost cover the region. Local changes of the pictures given in those works are commented upon under each species. In Ch. 8 I refer to all distribution maps known to me of the actual species, and list for Scandinavia the provinces from which a taxon is known. Nor have I found it necessary to publish complete lists of all herbarium material seen. The Appendices include the specimens employed in diagrams, illustrations and maps.

All microscopical observations were made in a Wild M 20 binocular microscope. For measurements up to c. 0.2 mm a 10× ocular with a scale divided into 100 parts was used. For measurements approximately between 0.2 and 10 mm I used a hand-lens (10×) graduated into tenths of mm, and above c. 10 mm a ruler graduated into mm.

For some special matters, not least concerning introduction and dispersal, I am forced to use terms that are unusual in English. Unless otherwise stated I have followed Jackson (1928) both as to the general sense and the linguistic form.

The disposition of the subject would be evident from the list of contents. I will emphasize, however, the role of the Conspectus as a summary with references to the previous chapters. Besides that a short summary of facts not possible to include in the Conspectus terminates the text.

II. CYTOLOGY

The *Cruciferae* is not a family that has been particularly attractive for cytologists. In most genera the chromosomes are too small to permit detailed individual analysis (cf. e.g. Manton 1932). Particularly concerning meiosis difficulties of preparation seem to arise also from the special chemical nature of many Crucifer plants. The most comprehensive surveys and discussions of chromosome cytology in the *Cruciferae* are still the works by Jaretzky (1928, 1932) and Manton (op. cit.). After that cytological observations have been included in the taxonomic treatment of several genera and species groups, e.g. in *Erophila* (Winge 1933, 1940), *Biscutella* (Manton 1934, 1937), *Rorippa* sect. *Cardaminum* (Howard & Manton 1946), the *Cardamine pratensis* complex (Lövkvist 1956). One survey of the chromosome numbers of Canadian *Cruciferae* has recently been started (Mulligan 1964, 1965, 1966). Another comprising American species was published by Rollins (1966).

Previous information about sect. *Rorippa* is chiefly restricted to somatic chromosome numbers given in various papers. In five cases (Jaretzky 1932, Scheerer 1939, Howard 1947*c*, Raj 1965 and Rollins 1966) meioses were investigated. References to all these papers are given in Table I and in Ch. 6 (cf. also Löve & Löve 1961).

Methods

The primary aim of the cytological work was to determine the chromosome number in a material comprehensive enough to permit conclusions on the occurrence and distribution of cytotypes. This was achieved through studies of mitoses in root-tips, which were generally taken from pots in the experimental garden. As a rule the chromosome number was checked in all plants within a sample (cf. p. 14). The root-tips were fixed in chrome-acetic formalin (Navashin's fluid, modified according to Müntzing 1933), embedded in paraffin, sectioned, in general at 14μ, and stained in 1 % solution of gentian violet. In a few cases mitoses were also checked in tapetum cells of anthers in connection with meiotic preparations.

Meioses were studied on a limited scale on objects thought to be of special interest. Whole inflorescences in buds were fixed, usually in Carnoy's fluid. In the large flowered species meioses were generally found when the anthers were about 0.5–0.8 mm long, but in *R. islandica* and *R. palustris* in anthers smaller than 0.5 mm. Various methods of staining were attempted but failed more or less

Table I. Survey of species and spontaneous hybrids represented on the various levels of polyploidy in sect. *Rorippa*.

Species within brackets belong to the *Rorippa pyrenaica* group (cf. p. 10). Five of the references concern meioses (cf. p. 16).

Diploids (2n = 16)	
R. amphibia (L.) Besser	Howard 1947*c*. App. 1
R. austriaca (Cr.) Besser	Manton 1932, Howard 1947*c*. App. 1
R. barbareifolia (DC.) Kitagawa	App. 1
R. curvipes Greene	Rollins 1966. App. 1
R. curvisiliqua (Hook.) Bessey	Mulligan 1964, Rollins 1966. App. 1
[*R. icarica* Rech.fil.]	App.1
R. islandica (Oed. ex Murr.) Borbás	(Jaretzky 1932?), Löve & Löve 1956, Jörgensen, Sörensen & Westergaard 1958. App. 1
[*R. pyrenaica* (Lam.) Rchb.]	Manton 1932. App. 1
R. sessiliflora (Nutt.) Hitchcock	App.1
Triploid (2n = 24)	
R. amphibia × *palustris*	Howard 1947*c*
Tetraploids (2n = 32)	
R. amphibia (L.) Besser	Wulff 1939, Löve & Löve 1942. App. 1
[? *R. lippizensis* (Wulfen) Rchb.]	cf. Jonsell 1964.
R. palustris (L.) Besser	Scheerer 1939, Howard 1947*c*, Jörgensen, Sörensen & Westergaard 1958, Mulligan 1964, Raj 1965. App. 1
R. sylvestris (L.) Besser	K. Larsen 1956 (cf. p. 86), Jonsell 1964. App.1
R. amphibia × *palustris*	App.1
R. amphibia × *sylvestris*	App. 1
R. austriaca × *sylvestris*	App.1
Pentaploids (2n = 40)	
R. sylvestris (L.) Besser	Jonsell 1964. App. 1
R. amphibia × *sylvestris*	App. 1
Hexaploid (2n = 48)	
R. sylvestris (L.) Besser	Howard 1946, Löve & Löve 1956, Jonsell 1964. App. 1

completely, among others Feulgen and orceinic methods. Results were only obtained from staining in carmine, to some extent in acetocarmine, but particularly in alcoholic hydrochloric acid-carmine, a method described by Snow (1963), which I followed with slight modifications. The material was easily squashed and the preparations were made permanent through freezing on dry ice.

Results and discussion

The basic chromosome number of *Rorippa* is $x=8$, a common number in the *Cruciferae*. Within the section *Rorippa* moderate polyploidization occurs. Tetraploid cytotypes are known within three species, hexaploid only in one (see Table I). A triploid and some pentaploids are clearly derived from crosses between the levels mentioned. From crosses involving pentaploids aneuploid plants arise. Such have not, however, been found in nature.

In mitosis the chromosomes are very small, as a rule 1–3 μ long at metaphase. Their shape is mostly straight, sometimes slightly curved, rarely strongly bent (see Plate I, A–F). These differences in shape seem to depend upon the stage of constriction, and no easily recognizable chromosome pairs were seen anywhere. In one and the same plate the length of the longest chromosomes may be about twice that of the shortest, but in most cases the differences are more subtle.

Diploids. In the diploid taxa (cf. Table I) I tried to find out whether it was possible to recognize characteristic idiograms in the mitotic metaphases. No reliable differences were revealed, and in some cases the intraspecific variation was found to be greater than the interspecific. The most characteristic feature observed is the occurrence in a few cases of chromosomes carrying satellites, e.g. in the Scottish *R. islandica* (J 944), where all the plants raised from seeds showed one pair of chromosomes with a satellite each. In *R. islandica* of other origin no satellites were seen. In *R. austriaca* a pair of chromosomes with satellites was seen in the two samples investigated, J 1552 (Denmark) and J 1123 (France). In the first case all material belonged to a single clone, but in the latter a number of plants raised from seeds showed the same structure.

Meioses were checked in *R. amphibia*, *R. austriaca*, *R. curvipes* and *R. islandica* (J 1271, 1123, 1286, 721 resp.). In all cases the number $n=8$ was found and no irregularities were observed.

Tetraploids. In the three species containing tetraploids (Table I) very few discrepancies from the exact mitotic complement of $2n=32$ were found. From seed samples of spontaneous *R. sylvestris* a few aneuploids ($2n=31$, 33 and 37) appeared besides normal tetraploids (cf. p. 20). In *R. palustris* J 1131 a fragment, about half the length of the shortest chromosome and normally stainable, was found to be added. Fragments of similar size are somewhat more common in the tetraploid hybrids (J 933*b*, J 1168*a*), but not more than one in each plate. Since these fragments are markedly shorter than any chromosome they cannot be interpreted as supernumeraries, but have probably arisen after meiotic fragmentation, perhaps of a univalent.

Only few meioses were seen of tetraploids, but those of *R. palustris* were quite regular. In spontaneous tetraploid hybrids (J 371, 541, 868, 1220) some disturban-

ces were seen, viz. one or two small laggards (probably whole or divided univalents) in many PMCs in the stages M I–A I. But in many cases the course seemed to be quite normal, which is to be expected since viable pollen is produced by those plants in considerable amounts (cf. Table V). The completely failing meiosis in the *R. sylvestris* clone J 186, leading to the production of nonaperturate pollen is treated on p. 91.

Tetraploids produced from controlled crosses, e.g. those resulting from backcrosses of *R. austriaca* × *sylvestris* to *R. sylvestris*, showed on the whole very regular divisions in the PMCs. In the hybrids *R. amphibia* × *palustris*, however, laggards were frequently observed in A I, but in M II the number $n=16$ was possible to establish in some cases. In spite of that a very low percentage of the pollen of the actual plants (from the cross J 379 × J 471) seems viable (cf. Table V, Plate I, J–K).

Hexaploids. In spite of the rather high level of polyploidy and the strong vegetative propagation in the actual plants, the number $2n=48$ was found to be exact throughout the spontaneous hexaploids. In a few cases one or two fragments of the type described above were observed, notably in the clone J 1082, which is of special interest (cf. p. 94).

Considerable meiotic instability was noticed in all hexaploids examined. The course M I–A I in a large number of PMCs showed one or two probable univalents lagging behind. Such clones (J 188, 1109) produce irregular but partly functionable pollen (cf. p. 30). Total inhibition of meiosis, with apparent failure in formation of at least diakinesis and subsequent stages was observed in clones known to have nonaperturate pollen (J 171, 877, 886, 963, 1083, 1113).

The meioses in the progeny from a cross between two hexaploids with irregular pollen (J 531 × J 188) was irregular in a still higher degree than in the parent clones (Plate I, H–I). The number of laggards was up to five in one PMC during M I–A I, and there were also portions too large to be univalents left behind in A I. The meioses of *R. sylvestris* are sometimes irregular already on the tetraploid level, but those of the hexaploids seem as a rule to be rather seriously disturbed in a degree quite surpassing what is known within any other euploid cytotypes of the species studied. This matter will be discussed below in connexion with other data on hexaploid *R. sylvestris* (Ch. 6 B, cf. Table IV).

Triploids and pentaploids. The only spontaneous *triploid* known, *R. amphibia* × *palustris*, was cytologically studied by Howard (1947*c*). He reported that 7–8 bivalents and 8–10 univalents were to be seen in the PMCs. This situation apparently provokes complete male sterility. In the artificial triploid *R. austriaca* × *sylvestris* (as well as in the best preparations from the spontaneous tetraploid samples of this hybrid) one chromosome with a satellite, evidently from *R. austriaca*, is visible in mitotic metaphases.

In the *pentaploids*, only a small number of which have been found, chromosome fragments were seen in the mitoses of some of the *R. amphibia* × *sylvestris* hybrids (J 1091*b*, 1091*k*, 1312). The meiotic course in J 1091 is very variable and there are usually both larger aggregates, possibly trivalents, and probable univalents present in M I–A I. In one pentaploid *R. sylvestris* (J 865) not even initiating meioses were seen in the PMCs, which later on shrivelled. J 865 is the only spontaneous pentaploid seen where meiosis is so disturbed as to lead to complete male sterility and apparently also female sterility.

The pentaploids produced from crosses within *R. sylvestris* (hexaploids × tetraploids, cf. Ch. 5) show sometimes a small fragment in the mitotic divisions, indicating meiotic irregularities. In interspecific crosses between these levels, i.e. *R. amphibia* × *R. sylvestris* no fragmented chromosomes were seen. Mostly the number was exactly $2n=40$, but in some cases one chromosome was missing or supernumerary. The intraspecific cross seems here to give products with a more irregular course than the interspecific one, which might be due to the occurrence of a greater number of nearly homologous chromosomes in the former case.

Aneuploids. The aneuploids raised from spontaneous seeds include three plants of *R. sylvestris*, with $2n=31$ (J 1587*c*), $2n=33$ (J 1135*a*) and $2n=37$ (J 1074*b*), all of French origin. The meiosis of the first one is rather regular. In some PMCs a small supernumerary chromosome was seen, which is perhaps only a part of a univalent. The root-tip mitoses of J 1135*a* show a supernumerary chromosome of normal size (cf. Plate I, D). Other aneuploids were raised from spontaneous seeds of pentaploid *R. amphibia* × *sylvestris* hybrids (J 1091). Their mitotic numbers vary from 33 to 38. The aneuploids raised from crosses of pentaploids with tetra- and hexaploids cover the whole range $2n=33$–39 and $2n=41$–47 respectively. After free pollination of a tetraploid *R. amphibia* × *sylvestris* hybrid (J 356) one plant with $2n=31$ and one with $2n=55$ were obtained. In a few aneuploids small fragments could be seen at mitoses, but most plants contained only complete chromosomes.

The meioses show here, as expected, frequent occurrence of univalents and of probable trivalents etc. as well as of interrupted courses. The examples studied represent only a small fraction of the material, but it seems obvious that meiotic course in the aneuploids is not more irregular than in the hexaploid *R. sylvestris* clones. In the abnormal plant with $2n=55$ meiosis was fulfilled up to T II, but a number of fragments were at this stage excluded from the forming nuclei. No viable pollen was produced.

The geographical distribution of cytotypes is discussed in Ch. 6.

III. MORPHOLOGY

This chapter gives a general morphological survey of organs of importance for the studies of variation within and between taxa. Phenotypic variation and other circumstances influencing the evaluation of characters will be treated.

Vegetative organs

Subterranean organs and life-length

I have studied the subterranean organs mainly in the field, since their free development is prevented in cultivation. Anatomical preparations were in many cases necessary for a reliable determination of their nature.

The root systems of *R. islandica* and *R. palustris* consist of a tap root that may become branched but that does not expand considerably laterally. Under exceptional circumstances, adventitious shoots may be formed, e.g. when roots in loose substrate come close to the surface or in detached plants floating in drift. During the first year *R. amphibia*, *R. austriaca* and *R. sylvestris* also develop branched tap roots only. The following years especially *R. sylvestris* and *R. austriaca* form lateral roots from which adventitious shoots arise. The two latter species and their hybrids have far creeping branching roots, which can effectively penetrate a wide area, give rise to numerous shoots and contribute to dispersal (cf. Ch. 4). At least in *R. sylvestris* the adventitious shoots seem to be formed where the roots run near or above the surface. If the primordia are covered by soil the rising shoots can, however, penetrate a layer of at least 10 cm depth (cf. also Kopecký 1965*a*). The formation of adventitious shoots in *R. austriaca* was studied by Wilson (1927), who found them to be exogenous, an exceptional behaviour.

R. sylvestris and its hybrids have also subterranean parts of stems, which do not lie far below the surface but through the formation of adventitious roots may become similar to the creeping roots. The transition to basal parts of ascending green shoots is continuous. In *R. amphibia*, where owing largely to the type of habitat no subterranean stem portions occur, the bases of the tall and hollow flowering shoots are generally prostrate and rooting. From these annual shoots axillary new shoots are formed as leaf-rosettes towards the end of the season, and from those new floral shoots may arise the following year. In that way *R. amphibia* clones expand to form large clumps on banks of drift and similar places. Since primarily prostrate non-floral stems have not been observed in these

Rorippa species, the term "rhizome", which is sometimes seen, would here be inadequate.

The seedlings of *R. islandica* and *R. palustris* proceed directly to flowering. The floral shoot may form a number of buds in the axes of the ephemeral rosette leaves. These buds, which are situated approximately at the soil surface, hibernate and then give rise to new floral shoots. Such buds seem to be rarely generated in *R. islandica*, which is accordingly mostly annual, but are common in *R. palustris*. In that way the latter species may perennate but all the same the plants are not long-lived. No plant survived more than 4–5 years in cultivation. Individuals from N. Fennoscandia tended to perennate better than plants from more southern regions.

The other species and their hybrids form the first year a strengthening stage consisting of a leaf-rosette. Only in exceptional cases have weak floral shoots arisen from such rosettes towards the end of the first season. During the following years usually a number of annual floral shoots rise from the place of the declined rosette. The individuals that expand by means of roots and/or prostrate stem portions would have practically infinite life-length.

The species mentioned are hemicryptophytes (s. Raunkiær 1907), except *R. islandica*, which seems mostly to be a therophyte.

Stem

Height, branching and mode of growth are the most important characters offered by the stem. The genotypic variation on these points is considerable, but, as concerns intraspecific variation, it is covered by modifications, whose effects are here particularly drastic. Height and branching are most affected. In the well perennating species these features chiefly vary with the moisture conditions. Especially *R. amphibia*, which can grow in both aquatic and terrestrial habitats, produces much shorter and less branched stems if growing constantly under terrestrial conditions, as it mostly did in cultivation, also if the pots were kept in water. For optimal development *R. amphibia* seems to claim deeper water, at least during the period when the floral shoots rise, and possibilities for the roots to expand freely.

In the short-lived species the stems of the seedlings are easily modified at least by light conditions and substrate moisture. Moderate shade (shadowy part of greenhouse) seemed to provoke branched and low stems in *R. palustris*, while seedlings from the same seed sample raised in open places outdoors were branched only higher up. In the dry places where *R. palustris* often grows adventitiously, the plants are erect, slightly branched and rather tall (cf. Ch. 6 A). Extremely low plants (in flower smaller than 5 cm) often appear late in the summer from seeds produced the same season. Older individuals of *R. palustris* may especially in well nutritious soil or on river shores, not least where boulders offer a shelter, consist of

numerous richly branched stems, nearly 1 m tall (J 142, cf. also Sylvén 1915). Such individuals produce innumerable seeds, which germinate to plants of quite ordinary appearance, which proves that these giant specimens are modifications.

On a smaller scale the same was observed in *R. islandica*. The plants J 1046, collected in a potato field, had about twelve vigorous flowering branches diverging from the base, while in normal habitats not more than about five branches are formed. Under severe conditions, as sometimes in Greenland and in the Alps, the stems of *R. islandica* may be very low (below 5 cm) and concealed among the rosette leaves.

The ascending to erect mode of growth which at flower time is normal in cultivation in the N. W. European species except *R. islandica* and many clones of *R. sylvestris* is seen under most conditions in nature. Accidentally stems may become depressed towards the ground and even produce adventitious roots (cf. also p. 21), which in *R. palustris* has evidently led to unjustified description of *formae* (e.g. Lakela 1948).

From this account it is evident that the gross morphological characters supplied by the stem should only be considered in a material cultivated under fairly equal conditions.

Foliage

The leaf-shapes range from non-lobate in *Rorippa amphibia* and *R. austriaca* to deeply lobate in *R. sylvestris*. The lobate leaves will be characterized as "pinnatifid" (e.g. Fig. 18, G–K) or "pinnatisect" (e.g. Fig 12), which is chiefly in accordance with Clapham, Tutin & Warburg (1962). I will also employ the term "lyrate" (e.g. Fig. 15, F). The portions of the leaves will be called segments, lateral and terminal. The term "pinnate" will not be used here, since not even in *R. sylvestris* are the leaf-segments completely free from each other but united by narrow stripes along the mid-vein. Apart from the cotyledons the leaves fall into three unsharp groups: rosette leaves, cauline leaves and leaves subtending the inflorescences.

The cotyledons seem to have a shape characteristic of each species. They are, for instance, oblong in *R. sylvestris*, orbicular in *R. palustris*, and orbicular except an obtuse-angled apex in *R. islandica*. The intraspecific variation of the cotyledons is small.

The rosette leaves are ephemeral in all taxa treated here (cf. Ch. 8). They generally disappear during the stretching of the first floral shoots. In *R. palustris* and especially in *R. islandica* they may, however, persist during anthesis. In the truly perennial species rosettes are also formed from shoots on roots or from decumbent stem portions. As a rule the rosette leaves are somewhat more dissected than the cauline ones, which is particularly evident in *R. austriaca*, where the latter are

always non-lobate. In *R. palustris*, *R. islandica* and *R. sylvestris* the segments are often deeply lobate but exceptionally even entire rosette leaves may occur. Rosettes of *R. amphibia*, which are frequent on prostrate stems, have usually lyrate leaves (cf. Ch. 6 C).

Between cauline leaves and leaves subtending inflorescences no sharp limits at all exist. The leaves become narrower and less lobate towards the upper parts but the chief specific characteristics are maintained. The following account will mainly treat of the well developed leaves in the lower and central parts of the stem.

Important is the variation in lobation, which chiefly implies that the terminal segment may become larger and wider, while the number of lateral segments is reduced. This can be simply expressed as the length of the terminal segment in relation to the total length of the leaf or as the number of pairs of lateral segments. The first method was used in Fig. 17, the latter was chosen for Fig. 9. For hybrids I did not in general find it possible to cover leaf-variation with simple measurements or an index, but preferred illustrating the leaf silhouettes (Figs. 18, 19, 20, 22). Such were drawn also for material used in diagrams, since e.g. the shape of segments and margins are also of importance.

Phenotypic leaf-variation owing to nutritional conditions results chiefly in size-changes and the shape is not markedly altered. In *R. amphibia*, however, the leaves become more acutely serrate in drought. Light conditions have more pronounced effects. In artificial greenhouse light the leaves of *R. palustris* and *R. islandica* became divided into a greater number of segments and those of *R. amphibia* became lobate higher up along the stem than is usual in nature. Plants growing in shade, especially in dense vegetation, have their leaves less deeply lobed. Particularly in *R. sylvestris* such specimens have often been mistaken for hybrids when found in herbaria. Confusion has also been caused by single specimens of *R. palustris* with non-lobate leaves that have probably originated during submersion.

Except for slight differences according to the position on the stem, the cauline leaves are generally very similar to each other. *R. amphibia* is an exception, since the early leaves are pectinate, the later ones nearly entire (see further Ch. 6 C).

The petioles are generally indistinctly delimited from the laminae, and have always been included in the leaf-length. The lamina may attenuate into wings (which in *R. islandica* and *R. sylvestris* may be very narrow) or the leaves may be sessile. Tendencies to auricles can be seen in all the species as slight widenings of the petiole at the stem, but only in *R. palustris* and, especially, *R. austriaca* are the auricles prominent. The upper leaves may lack auricles in contrast to the lower ones. In plants from unusually dry habitats they are often reduced or even absent. In *R. austriaca*, however, large auricles seem always to be present at least in most leaves. The auricle size is a good leading character especially for the evaluation of hybrids. For tabulation of this character the specimens were distributed into five classes according to the degree to which auricles were developed (cf. Table V).

In leaf axils the first leaves of new branches, which are mostly not further developed, form small rosettes and have shapes similar to the basal rosette leaves.

In recent times stomata and their guard cells have often been used for taxonomic purposes. On the infrageneric levels particularly their sizes have been employed as indicators of various polyploidy levels. They are, however, known to be much more susceptible to environmental modifications than the pollen grains (cf. below), as was clearly demonstrated by Brandt (1961). If taken from corresponding parts of an organ they may reveal polyploidal differences within a material cultivated under fairly uniform conditions, but this picture may be totally effaced in herbarium material. I have only in passing studied the stomata in comparisons between *R. islandica* and *R. palustris* and between the cytotypes of *R. amphibia*. The differences in my cultivated material tend to be smaller than those reported by Brandt (op. cit.) for his cytotypes of *Veronica prostrata* L., and in spontaneous material the differences break down.

Indumentum

The indumentum consists of hairs, sometimes similar to minute scales. Only simple hairs occur in the species treated, and no more specialized types have been reported from the genus. In Europe all the taxa treated are practically glabrous. They have, however, nearly always (except in *R. sylvestris*) a few hairs at the bases of petioles and often at the lower side of petioles and leaves, particularly when they are young. Especially in *R. amphibia* the young leaves may be conspicuously pubescent. Along the lowest part of the stem hairs are not rare either. In *R. islandica* and *R. palustris* and sometimes in *R. sylvestris* a few small hairs are present on every sepal.

The shape of the hairs was chiefly studied on the stem. These hairs are usually 0.3–0.5 mm long, unicellular, 30–50 μ broad at the base, and gradually tapering towards the apex. The walls do not exceed c. 8 μ thickness and hence the lumen is large. Variation between the species is small and the other types seen in European plants are probably only reductions or other alterations of the common type. The *R. amphibia* hairs are more broadly triangular in sectional view and have very narrow walls (3–4 μ). The *R. amphibia* hybrids show transitions. Strange, however, is a pentaploid *R. amphibia* × *sylvestris* hybrid (J 1091), where many of the hairs have a septum in the proximal part or at the middle. Some of these hairs have a rounded apex and are shorter than usual, others are of normal length and acute. They can therefore not be regarded as a distinct type of hairs, but are rather aberrants of the unicellular ones. They are worth mentioning since bicellular hairs have been regarded as not to occur in the *Cruciferae* (Metcalfe & Chalk 1950).

Some stem hairs have in many plants the shape of very small scales. In *R. austriaca* × *sylvestris* only such hairs occur. They are very small (c. 0.1 mm)

and broadly triangular. They are, however, frequent and as far as known always present along the lowest part of the stem. This seems to be a distinguishing character against the *R. amphibia* hybrids, which have a dominance of normal hairs of various sizes.

In the North American populations of *R. palustris* the pubescence is often very conspicuous. There is a variation from virtually glabrous specimens to those with frequent hairs even along the raceme axes (notably ssp. *hispida*). The hairs are of the same type and size as described above in European material. The frequency variation is correlated with other features and is of taxonomic significance (cf. Ch. 6 A). In a Beringian species of close affinity to *R. palustris*, *R. barbareifolia* (cf. p. 84), the pubescence is still denser than in ssp. *hispida*. The hairs seem partly to be of another type, however. The dominant ones are much longer (c. 2 mm), c. 50 μ broad, taper only near the apex and have thin walls and a rather scale-like consistency.

I have studied variation in pubescence in a larger material only in the comparisons between European and N. American *R. palustris* (cf. Ch. 6 A, Fig. 9).

Reproductive organs

Inflorescence

The inflorescences are the racemes typical of the *Cruciferae*. They terminate as a rule the growth of all shoots, but are also formed in the axils of upper leaves and are often branched. In the fruiting stage there are marked differences between the species as to the stretching of the axis. In *R. amphibia* the axes become particularly elongate, in *R. sylvestris* they are sometimes flexuous in a zigzag like manner. The pedicels of ripe pods stretch to a rather definite length, but the variation amplitude within the same raceme is often about $\pm$ 25 %. The pedicels are often longer in the shade, i.e. also in the small racemes or single flowers found in the lower parts of many specimens.

The direction of the pedicels is often significant. They may be patent, as e.g. in *R. austriaca* and its hybrid, which here means a deviation from the axis of c. 45–70°. They may also be either horizontal or deflexed. The latter type is pronounced in *R. amphibia*, where the pedicels are gently curved downwards from $\pm$ horizontally inserted bases. Especially in *R. palustris* this character shows great intraspecific variation. These distinctions hold good only in fertilized pods.

In the tops of the inflorescences that happen to come into contact with a substrate new leaf-rosettes may be formed, a phenomenon observed several times towards the end of the vegetation period.

Petals and sepals

The four petals are yellow in various hues, from pale yellow in *R. palustris* to deep yellow with an orange tinge in *R. amphibia*. The yellow colour may some-

times dominate also in the sepals, particularly in *R. sylvestris*. The petal length is very variable, from 1.0 mm in *R. islandica*, to more than 5.0 mm in *R. amphibia*. The shape is less variable and there is usually a markedly broader lamina patent from the claw. This differentiation is less manifest in the small petals of the *R. islandica* group, and in *R. sylvestris* rather long and narrow ones may occur (cf. p. 95). The four sepals, which are slightly saccate, vary within narrower limits along with the petals. In the *R. islandica* group, however, the corolla is about as wide as the calyx, while in the other species the corolla is markedly wider.

I have frequently used the lengths of petals and sepals to illustrate intra- and interspecific variation, since these characters are little modified and easily accessible in herbarium material. Plants growing under markedly drier conditions than normal, as was sometimes the case with *R. amphibia* in cultivation, may obtain smaller petals. It is more important, however, that within a plant there is a gradual decrease in flower-size, especially petal-length, when fruit ripening begins. The anthesis is often finished by microflowers, lacking nearly all organs except the ovary. All measurements in flowers were therefore performed in specimens collected in full flower and before any pods had ripened. Under such conditions the variation amplitude in a specimen rarely exceeds $\pm$ 10 % and is often smaller.

Nectaries

The nectaries of the *Cruciferae* were objects of detailed studies and discussions during the end of the 19th and the first decades of the 20th century. The main purpose was to find new ways to a natural classification within the family (cf. Ch. 1). More recently the nectaries have been used for taxonomic purposes e.g. by Snogerup (1967) in *Erysimum*. Nectaries of *Rorippa* species have been described and illustrated by Velenovský (1883) (whose pictures were reproduced by Schweidler 1911), Hayek (1911) and Villani (1912). All the species of the section *Rorippa* have the same general arrangement with nectaries at the bases of both the longer (median) and the shorter (lateral) stamens. The latter are most prominent and surround the bases of the lateral filaments. From these lower strands of nectarial tissue proceed outside the median filaments.

There are clear differences between the species especially concerning the large nectaries at the lateral stamens, but the distinctions illustrated by Velenovský and Villani (op. cit.) do not hold in detail because the intraspecific variation is considerable. In *R. sylvestris* the nectaries around the lateral filaments form a closed circle, in *R. amphibia* they are horseshoe-shaped with the opening directed inwards. In *R. austriaca* they are also horseshoe-shaped but the tissue is very thin at the outer side of the filaments. In *R. palustris* the nectarial tissue is not coherent but there are rather wide openings both at the inner and outer sides of the filaments. The hybrids show often intermediate arrangements, which have been

of some value for the determinations. Also in the *R. pyrenaica* group the same general nectarial organization is found, while sect. *Cardaminum* lacks nectaries around the median filament bases (cf. Ch. 1).

Stamens and pollen

Stamens. The stamens are slightly tetradynamous with the lateral pair about 4/5 of the length of the four median stamens. Staminal length is on the whole coordinated with sepal and petal lengths and is thus of little importance as an independent character. In *R. palustris*, however, the relations between staminal and petal lengths may vary, so that in some populations the longer stamens slightly protrude from the flowers. In the special case of male sterility in *R. sylvestris* (cf. below and Ch. 6 B) the stamens are considerably shorter than normal (2.5–2.7 mm against 3.0–4.0 mm). The reduction affects almost totally the filaments, while the anthers have about normal length but are narrow.

Methods for pollen studies. For studies of fertility and for size measurements of pollen grains preparations were made in lactic blue, or in the latter case, also lactophenol. The percentage of grains with deep blue-stained plasma in a sample of about 200 grains was taken as a measure of pollen fertility. The size measurements comprised 25 grains in each sample and concerned always the equatorial diameter, which within each plant is less variable than the polar axis. The measurements used for comparisons (Table II) include only tricolpate grains. For calculations of the "mean" number of colpi (cf. below) c. 200 grains were investigated. More detailed morphological observations were made in pollen grains prepared with the acetolysis method described by Erdtman (1952). At acetolysis the grains swell more than in lactic blue and measurements in the two types of preparations are therefore not comparable. Pollen sections (0.1 μ, stained in basic fuchsin) of *R. sylvestris* and its hybrids, as well as some of the usual acetolyse preparations were made at the Palynological Laboratory, Stockholm-Solna, where voucher slides are preserved of the following numbers: J 143, 171, 188, 877, 1114, 1123, 1129, 1220, 1234.

Colpate pollen. Cruciferae is known as a "stenopalynous" family (Erdtman 1952), i.e. with little variation in pollen morphology between various genera. All normal grains of the actual *Rorippa* species are of the kind characteristic of the family: spheroidal, of medium size (polar axis c. 20–30 μ), tri- or tetracolpate, with a reticulate sexine that is much thicker than the nexine, and simplibaculate (Plates II, A–D and III, A; terminology acc. to Erdtman 1952). The pollen shows no clear specific characteristics, but there is a tendency in *R. amphibia* to thicker exine than in the other species.

Between the closely related diploid *R. islandica* and tetraploid *R. palustris*, as

Table II. Equatorial diameters of tricolpate pollen grains in *R. islandica*, *R. palustris* and *R. amphibia*.

The values are averages of 25 measurements.

Collection	Diameters (μ)
R. islandica ssp. *islandica*	
(Atlantic specimens)	
1934 Taylor (BM)	19.31 ± 0.13
1933 Paton (BM)	20.73 ± 0.14
J 1212	20.83 ± 0.17
J 1058	21.45 ± 0.17
J 721	21.54 ± 0.15
J 778	21.73 ± 0.15
J 977	21.78 ± 0.18
J 1046	21.78 ± 0.20
J 1055	21.93 ± 0.17
J 672	22.15 ± 0.20
J 944	22.25 ± 0.12
J 681	22.49 ± 0.19
1884 Jensen (C)	23.25 ± 0.15
(Central European specimens)	
1878 Willmott (K)	18.83 ± 0.17
1944 Becherer (G)	19.40 ± 0.19
1898 Chenevard (G)	19.50 ± 0.15
1945 Becherer (G)	20.02 ± 0.17
1882 Cornaz (G)	20.07 ± 0.17
1872 Bordère (K)	20.59 ± 0.22
Savoie 1904 Briquet (G)	20.92 ± 0.17
Valais 1904 Briquet (G)	21.02 ± 0.13
Bourgeau (K)	21.11 ± 0.18
1920 Briquet (G)	21.54 ± 0.13
R. islandica ssp. *dogadovae*	
Dogadova & Tzvelev No. 852 (BM)	20.49 ± 0.25
1924 Vereshczagin (LE)	20.54 ± 0.15
1921 Wysocz (LE)	21.11 ± 0.15
Becker (LE)	21.63 ± 0.23
Korovnik & Poyarkova No. 237 (LE)	21.77 ± 0.23
1916 Popov (LE)	22.11 ± 0.17

Collection	Diameters (μ)
R. palustris	
J 181	23.39 ± 0.23
J 855	24.24 ± 0.15
J 1460	24.49 ± 0.33
J 192	24.81 ± 0.19
J 169	25.00 ± 0.15
J 189	25.00 ± 0.18
J 193	25.00 ± 0.19
J 957	25.00 ± 0.26
J 174	25.14 ± 0.18
J 499	25.33 ± 0.18
J 1455	25.33 ± 0.24
J 1566	25.38 ± 0.24
J 1294	26.00 ± 0.20
J 403	26.38 ± 0.33
R. amphibia	
$2n = 16$	
J 1166	19.64 ± 0.17
J 1160	20.49 ± 0.13
J 1147	20.79 ± 0.17
J 1271	21.77 ± 0.13
J 952	22.91 ± 0.15
J 1462	23.06 ± 0.18
$2n = 32$	
J 376	24.86 ± 0.19
J 1175	25.62 ± 0.24
J 398	25.85 ± 0.22
J 1238	26.09 ± 0.24
J 352	26.14 ± 0.23
J 340	26.42 ± 0.16
J 353	26.66 ± 0.21
J 1142	26.90 ± 0.15
J 1099	27.28 ± 0.18
J 1188	27.28 ± 0.28
J 1100	27.56 ± 0.16

well as between the cytotypes within *R. amphibia* slight but evident size differences occur (cf. Table II), a matter often but by no means always observed in spontaneous polyploid series. Also the "mean" number of colpi rises in some cases distinctly with increasing polyploidy. In *R. islandica* almost all samples contain only tricolpate grains. In *R. palustris* there is a variation from almost purely tricolpate samples to those with a dominance of tetracolpate grains. Similar differences were found between the cytotypes of *R. amphibia*. In *R. sylvestris* tricolpate grains mostly dominate in the tetraploids, while grains with four or more colpi are frequent in the hexaploids (cf. p. 87). In some series of induced autopolyploids such increases in the number of apertures were reported by Maurizio (1956) for species of *Nicotiana*, *Trifolium* a. o., and by Bronckers (1963) for *Arabidopsis thaliana* (L.) Heynh.

Grains with more than four colpi ("pancolpate"[1]) are not rare in *R. sylvestris*, particularly not in the hexaploids. They may constitute about 5 % of the pollen (in J 1254 even c. 10 %). There are usually five equatorial colpi and additional non-equatorial ones (cf. Plate II, D). The equatorial diameters of these grains are c. 35μ, i.e. about 1.5 times as long as those of the tetracolpate grains. Their existence in hexaploid *R. sylvestris* is evidently another expression of the meiotic instability of that cytotype (cf. Ch. 2). Their sizes suggest them to be unreduced PMCs. A similar case was reported for *Caltha palustris* L. by Reese (1954) who could even from crossing results conclude upon the existence of unreduced PMCs in plants containing giant grains.

Pollen with normal exine, but 0–2 colpi was also seen, notably in *R. sylvestris*, but these grains are dwarfed and empty. Sterile pollen mostly retains the normal exine pattern, and only in some clones of *R. sylvestris* and its hybrids is the pollen partly or totally amorphous. A very special, aberrant type of sterile grains occurs, however, in some clones of *R. sylvestris* and will here be described in some detail.

Nonaperturate pollen. Erdtman (1958) discovered an aberrant type of pollen grains in *R. sylvestris* and described them as inaperturate,[2] subspherical, with an exine of obscure structure and a thin or even lacking nexine layer, which is on the whole confirmed by my own observations. They are, however, not always completely nonaperturate,[2] but there are grains with colpi of ± aberrant shape and localization. In surface view (Plate II, E–F) the exine has winding blunt ridges, reminding e.g. of the structure in the pollen of certain *Ulmaceae*. In many grains the exine looks extremely thin, and the grains are easily folded in preparations. In sections the bacula typical of normal grains are not seen. The exine has an

[1] This term is taken from Erdtman (1958).

[2] Erdtman (1958) used the term "inaperturat", but I prefer the synonym "nonaperturate" which is in accordance with Erdtman (1952).

amorphous, degenerated structure and may even be perforated (Plate III, B–C). The clearest distinction to the normal pollen is thus found in the exine structure. On this point the limit between the pollen types is sharp in all samples from spontaneous plants where distinct grains are formed. The aberrant grains will here with disregard of the exceptions mentioned be called "nonaperturate" in contrast to the "normal" or "colpate" grains. In e.g. some *Matthiola* species the pollen is normally nonaperturate, but the exine has a well-defined structure (Erdtman 1952).

No specimens producing both colpate and well-developed nonaperturate grains have been found among my spontaneous material, and in all cases the pollen type was constant throughout a clone, although certain anthers may form no pollen at all (cf. below). The diameter of the nonaperturate grains is somewhat variable, 22–30 μ (in lactic blue) except for single extremes. Erdtman gave (19) 24–32(41) μ for acetolyzed grains (cf. p. 28). The grains are less variable in some specimens (e.g. J 171 and the rest of this group, cf. p. 94), but of very irregular size in others, where the pollen formation has totally broken down in some anthers (J 963).

Already from their morphology it seems very plausible that the nonaperturate grains result from disturbances of the meiosis as suspected by Erdtman (1958). This view is confirmed by several other observations. The grains do not stain in lactic blue. The stamens producing such pollen are smaller than normal (2.5–2.7 mm long against 3.0–4.0) and do not open. The grains adhere moreover to each other and to the walls of the thecae if the anthers are broken. Also the other organs of the flower are unusually small (cf. Ch. 6 C, Figs. 10, 11). Erdtman's (1958) find of nonaperturate pollen in giant flowers would certainly be an exception, since no similar case is present in my material. Pollinations with nonaperturate grains have always failed completely. The nonaperturate grains are obviously completely barren and their exclusive occurrence in a clone implies total male sterility. The ovaries do not seem to be notably affected, however, since after pollination with normal pollen such male sterile plants yielded progeny in about the same degree as other crosses within *R. sylvestris* (cf. p. 91).

This progeny comprised plants with a highly variable pollen, but usually of low quality. Their colpate grains stain only to a low extent in lactic blue, and the nonaperturate grains have partly incomplete walls. Completely amorphous pollen prevails in a few specimens. In one plant, a pentaploid ($2n = 40$, with the hexaploid clone J 171 as the female parent) transitions between colpate and nonaperturate grains could be observed. Most grains were typically nonaperturate, some others had a reticulate exine pattern, but there were also grains without apertures but with thin reticulate walls and about the size normal for the nonaperturate grains. The pentaploidy of this plant may contribute to the situation, but a number of other individuals of the progeny with aneuploid numbers showed only one pollen

type. In progeny obtained from parents with only colpate pollen, nonaperturate grains were never observed.

In one of the spontaneous clones in cultivation (J 531) colpate pollen was sometimes formed but more often only empty grains with very incomplete walls approaching those of nonaperturate grains. In some thecae a coherent mass of giant "grains" (to 60 μ in diameter) surrounded by very thin if any walls were seen. This is perhaps a kind of syncytium formation as described e.g. in *Chaerophyllum* by Håkansson (1948).

Erdtman (1963*a*) reported transitional states without citing any examples, but he possibly hinted at the colpate pollen without distinct nexine found in two collections (one of those = J 539). In one case (J 253, from France) different pollen types were obtained in plants raised from seeds from a spontaneous occurrence. In all these plants there were a high number of badly developed or even amorphous grains.

In plants with nonaperturate pollen no meioses were discovered (cf. Ch. 2). In spite of the evident absence of nuclear divisions one, or sometimes two, septa are often formed across the PMCs (Plate III, D–E). The septa seem mostly to be incomplete and somewhat irregular, and the process is often interrupted before a complete tetrad is reached. The exine material seems to be deposited around the tetrad without being arranged into the normal characteristic pattern. The nonaperturate grains seem therefore normally to be unfunctionable PMCs of a special kind, but sometimes the elements of a tetrad separate and form each a smaller nonaperturate grain.

It seems plausible that the cause of this pollen anomaly is the mutation of a single gene, whose action is suppressed in progeny raised from seeds (cf. Ch. 6 B) rather than failures originating during the meiotic course. The fact that the two pollen types normally exclude each other in the clones supports this hypothesis.

In Ch. 6 B this pollen type is put in relation to the variation in cytotype and gross morphology and to distribution and ecology. It is shown there that this pollen occurs in plants of various cytotypes and morphotypes, where the anomaly has probably arisen independently.

Pistils and pods

In most Crucifer genera the pod-shape is a fairly constant character. In the section *Rorippa* the interspecific variation is, however, unusually wide. The extremes are found in the intercrossable species *R. austriaca* with spheroidal pods and *R. sylvestris* with linear ones, up to 20 times as long as broad (cf. Ch. 8). The ovaries of *R. sylvestris* are, however, only 3 to 4 times as long as broad. The intraspecific variation in pod-shape is also of taxonomic interest, especially in *R. palustris* (cf. Fig. 9). The size of the ripe pods may increase considerably with the rest of the plant in well nourishing habitats, at least in *R. islandica* and *R. palustris*,

but the shape is otherwise little influenced by environmental factors. These circumstances, together with the facility to study pod-shape in a large material, made it natural to employ the pods in a high degree for studies of the variation in species and hybrids, as far as the latter are fertile. Lengths (style excluded) and widths were employed as variates. When fully ripe the intraindividual variation of these measures does not exceed ± 10 %. In the herbaria ripe pods are, however, rare in the self-incompatible species, and data could then be obtained only from the cultivated plants. In herbarium material of these species, especially *R. sylvestris*, the lengths of the unfertilized gynecia, which grow out to a rather definite size, in relation to pedicel lengths furnished a suitable expression of intraspecific variation. There is, however, no special correlation between this character and the length of ripe pods.

The *valves* have usually a firm consistency, but are thin in *R. islandica*, a matter discussed in detail in Ch. 6 A (cf. Plate III, F–G). In spheroidal and stout pods one or two secondary ruptures are sometimes formed at dehiscence. During the 19th century this was thought to be a feature of taxonomic importance, and for the species *R. barbareifolia*, which has mostly four "valves" the genera *Tetrapoma* and *Tetracellion* were created (cf. p. 145). The phenomenon was discussed by Solms-Laubach (1900) and Gerber (1899). The latter denied its taxonomic value after having found pods with two to four valves in the same specimen of *R. palustris*. Borbás (1879*b*) reported about the same feature in a *Rorippa* hybrid.

The *replum* is thin and consists of irregularly polygonal cells of various sizes and with rather thick walls. It consists of two layers, each one cell-layer thick, which may separate from each other though held together by a thicker layer of tissue along the middle of the replum and by bundles that run along each margin. Repla from the actual species are very similar and so are those of sect. *Cardaminum*.

The *styles* vary with respect to both width and length, especially the latter. They are of special importance for studies of the interspecific variation (cf. Fig. 17). To obtain comparative values I have only measured style-lengths (stigmata included) in ripe pods. The stigmata are rather uniform in the N. W. European species. They are capitate and sometimes slightly bifid, but the variation was not possible to connect with other features. In N. American *Rorippa*, and already within *R. palustris*, the variation is greater, reaching from non-capitate stigmata, i.e. not wider than the style, to distinctly capitate ones (cf. p. 81). The stigmatal papillae are bottle-shaped and of the same type in all the species.

The ovaries contain about 25–70 *ovules* each. The ovules are most numerous in *R. palustris*, fewest in *R. amphibia*, but the variation is considerable within each species. Many ovules abort, especially in *R. sylvestris* and *R. amphibia*.

Seeds

There are many studies of various aspects of the seeds in the *Cruciferae* (cf. Netolitzky 1926). In this family the seeds often supply good diagnostic characters

also on and below the specific level, e.g. in *Arabis* (Rollins 1941), *Brassica* (Berggren 1962) and *Rorippa* sect. *Cardaminum* (Howard & Lyon 1950). Of special value is often the anatomy of the seed-coat, whose various layers were described and illustrated e.g. by Netolitzky (op. cit.), Černohorský (1947) and Berggren (op. cit.). *Rorippa* seeds are described in detail in Černohorský (op. cit.) and Murley (1951).

The seeds were partly studied in sections at 14–20 μ stained in safranin—light green. They have accumbent embryos, are devoid of wings, not even distinctly marginate, and have no mucilagenous substance of the outer epidermal cells. While the inner seed-coat layers are on the whole uniform, the outer epidermis differs between the species. The outermost wall of each cell is, however, nearly always slightly to distinctly convex, which makes the surface covered by low elevations. The surface appears somewhat different due to the different heights of these elevations, which induced Murley (op. cit.) to discern three types of surface patterns within the sect. *Rorippa*. Since there are no principal differences this does not seem justifiable. Černohorský (op. cit.) used the term reticulate for all species of *Rorippa* s.str. But in the N. W. European species the elevations do not constitute a network of the kinds found in other parts of the section, viz. the *R. pyrenaica* group, and in sect. *Cardaminum*. One of the terms used by Murley, "colliculate", i.e. with "rounded broad elevations, closely spaced, covering the seed-coat", seems most appropriate for all the species treated here.

In *R. amphibia* and *R. sylvestris* the outer epidermal cells are generally filled with a stainable substance, and the outer epidermal layer and its walls have a less regular structure than in the *R. islandica* group. There the cells are empty, have straight and often perforated transverse walls (a peculiar feature also remarked by Černohorský), and more regular shape and defined size. There are characteristic differences in size and shape between various taxa (cf. Ch. 6 A, Plate IV). In the *R. islandica* group the seeds are light brown owing to the air-filled epidermal cells, but reddish brown in the other species. Occasionally the outer epidermis is sunken or peels into flakes, which may give also to the seeds of the *R. islandica* group a darker brown colour.

The seeds vary considerably in size within each species. The lengths, which were always measured parallel to the embryo side, are given in Ch. 8. In spontaneous and artificial hybrids very small or partly filled seeds are often formed, which all the same may germinate (cf. Howard 1947*a*).

IV. REPRODUCTION AND DISPERSAL

Mating systems

The N. W. European species of *Rorippa* s.str. represent two sharply contrasting mating systems, viz. pronounced allogamy and equally pronounced autogamy. *R. amphibia*, *R. austriaca* and *R. sylvestris* are allogamous. Both in herbaria and in the field their seed setting is found to be poor. In the experimental garden with its supply of mixed pollen the plants normally set plenty of seeds. Isolation in bags of a number of *R. amphibia* and *R. sylvestris* clones and one clone of *R. austriaca* (J 1123) confirmed that they are highly self-incompatible. Many clones gave no seeds at all, but in a number of cases seeds were formed in some pods after isolation (J 890, 913, 961, 1123). These seeds germinated to plants of parental shape, and the self-incompatibility is hence not absolute in all clones. The hybrids between the species mentioned are also highly self-incompatible, but are comparatively often found with seeds in the field, since they often grow together with other biotypes.

No experiments have been performed to clarify the distribution and inheritance of the self-incompatibility factors. In cases where crosses failed between what would reasonably be different clones, cytological disturbances may be supposed to be the principal cause, e.g. in the clones of hexaploid *R. sylvestris*.

The flowers of the allogamous species are entomogamous.

The *R. islandica* group is predominantly autogamous. Here the anthers open at about the same time as or even before the buds, and are then mostly in contact with the stigma. Cleistogamic flowers were never observed, however. Isolated plants of *R. islandica* and *R. palustris* have always produced seeds in normal quantities. In a few cases (J 504, 1456) the haploid number of the megasporogenesis was established.[1] To judge from the variation pattern (cf. Ch. 6 A) and the very good pollen quality apomixis is highly improbable in the *R. islandica* group. The plants are probably practically always self-pollinated, which would lead to high homozygosis and "pure lines". The progeny raised from seeds, whether collected from a plant in the experimental garden or from a population in the field, is actually completely uniform.

[1] Whole racemes still in buds were fixed in Carnoy's fluid, embedded in paraffin, sectioned and stained in gentian violet.

Seed dispersal

In the *R. islandica* group the seeds are the sole important diaspores, while they play a more subordinate role in the allogamous species. The seeds have no special organization for transport, but through water, animals and not least human activity great numbers are effectively spread. In *R. islandica* and *R. palustris* a very high percentage of the seeds germinate, often about 90 % when sown on moist filter paper (cf. p. 14). In nature they may germinate the same season and give rise to small seed setting plants or only rosettes, which hibernate, but germination the following season is also very common. Sernander (1901) reported *R. palustris* to form hibernating fruit-stands "vinterståndare", which may occur only in very large and vigorous specimens. I have been unable to germinate *R. palustris* seeds older than five years and already after about two years there is a marked decrease in their ability to germinate.

In nature *R. amphibia*, *R. austriaca* and *R. sylvestris* set seeds practically only where different biotypes of the same or different species meet. Seed samples of these three species have very varying but usually considerably lower germination ratios than the *R. islandica* group, and hybrid seeds may germinate to the same extent as those of the pure species. Under non-weedy conditions seeds would have good chances of giving rise to plants only on open shores not too often disturbed but not in habitats with dense vegetation e.g. of large clumps of *R. amphibia*. The long time necessary for the seedlings to reach flowering should also be kept in mind (cf. Ch. 3). For the allogamous species the seeds are most important from an evolutionary point of view, as giving rise to new biotypes, while local dispersal is predominantly vegetative. But especially as weeds both *R. austriaca* and *R. sylvestris* and also hybrids between them are spread through seeds over long distances, as indicated e.g. by their occurrence at large mills (cf. Ch. 6 and App. 4, 6, 7).

Vegetative dispersal

The *R. islandica* group has no organization for vegetative dispersal. I have a few times seen small individuals of *R. palustris* floating in drift with adventitious shoots proceeding from the tap root (cf. Sernander 1901, p. 350), but this is quite exceptional.

The allogamous, perennial species have good capacities of regeneration from fragments of both roots and stems. In *R. amphibia* the basal, prostrate stems with their axillary buds are easily fragmented, and stem-portions with large buds are spread, especially at high water-level in the autumn and the spring. The diaspores may also consist of rather long new shoots arising from the buds mentioned or fragments of such shoots. Dispersal of *R. amphibia* has earlier been studied by Sernander (1901), who gave detailed and adequate observations from L. Mälaren, and by Zbořil (1919) and Kopecký (1965*b*).

In *R. sylvestris* stem-portions may also give rise to new plants but they are not so well organized for dispersal as those of *R. amphibia*. Most important for *R. sylvestris*, and probably also for *R. austriaca*, which I have not studied in natural habitats, is dispersal of fragments of the root runners, in which adventitious shoots may be present or formed later (cf. also Wittrock 1884, Salisbury 1961).

Under natural conditions only dispersal by means of water is imaginable for the vegetative diaspores, and those of *R. amphibia* with hollow stems and loose tissue are well organized for floating. Animal transports are probably exceptional. This may lead to marked isolation within a water system, especially in those cases where only one clone is present and hence no seeds that are more easily transported can be expected. The vegetative diaspores of those populations might, however, be transported by shipping within and between waters connected in that way. The possibilities of such dispersal in some special cases are discussed in Ch. 6.

Clones that grow isolated as weeds, which is common in *R. sylvestris* but not in *R. amphibia*, will not only for their claims of habitat but also for their dispersal be directly dependent on human activity. The plants must rely upon transports of their diaspores e.g. with soil. Dispersal in that way accounts for the rapid expansion in recent times of *R. sylvestris* both in Scandinavia (cf. Ch. 6 D, Fig. 13) and in U.S.A. (Stuckey 1966*a*).

Dispersal and population structure

The contrasting methods of mating and dispersal lead to extreme contrasts in the population structure of the actual species. In the *Rorippa islandica* group the population e.g. within a water system or even larger unities will tend to consist of genotypically very similar individuals. Where because of natural or anthropochorous dispersal clearly different biotypes of various origin meet variation in the region as a whole is conspicuous, but the local populations are all the same uniform, as judged from the conditions in N. Fennoscandia. It is also probable that the rare cross-fertilizations will only include very few ovules in a plant and therefore the new combinations would be infrequent in the progeny. Only where progeny from such a new combination succeeds in forming a population would an intraspecific "hybrid swarm" arise. A notice by A. E. Porsild (1951) from the Yukon Terr. of glabrous and pubescent specimens of *R. palustris* growing together may indicate that different biotypes had met and crossed. The ephemeral nature of most habitats of the *R. islandica* group reduce the chances that such "hybrid swarms" would persist in a locality long after crossing. Moreover, a local population is rarely rich in individuals and I have never seen these plants forming coherent vegetation.

The individuals of the allogamous species would be highly heterozygous and practically every seed might represent a new combination. These species will tend on the one hand to constitute populations rich in differing biotypes between which crosses occur, on the other to form populations consisting of a single clone.

Within a whole water system or an area held together by human communications a species may be represented by only one clone divided into numerous rhizoclones. Where two clones of good sexual capacity meet, the chances are great for new clones to be formed. Within a variable and complex species such as *R. sylvestris* conspicuous new combinations may result, which if vegetatively vigorous may obtain a foothold. In both *R. amphibia* and *R. sylvestris* there are examples of partially or totally sterile clones constituting whole local populations or even more. New clonal populations may arise from both intra- and interspecific crosses, the limits between which will become more arbitrary the more the hybrid clones take part. Special ecological claims and reduced vitality of many hybrid derivatives seem here to prevent the species from merging into one variable complex where they meet.

V. CROSSING EXPERIMENTS

Aims and methods

Crossing experiments were performed along two lines. One implied controlled crosses between certain plants in the cultivated material, the other free pollination between a great number of plants growing together in the experimental garden.

Crosses between species and/or spontaneous hybrids aimed particularly at getting some idea of the existence of genetic barriers. The F_1 progeny obtained would furnish material morphologically comparable with hybrids found in nature. The crossing experiments involved chiefly the species *R. amphibia*, *R. sylvestris* and *R. palustris* as well as hybrids. One clone of *R. austriaca* was also used. Self-incompatibility makes it easy to handle all material except *R. palustris* and *R. islandica*, whose pronounced autogamy, small flowers and early ripening pods cause considerable difficulties. *R. palustris* was hence successfully used only as the male parent, which would also be its predominating role if hybridizing in nature with the allogamous species mentioned. Intraspecific crosses were performed in *R. amphibia* and *R. sylvestris*, chiefly in order to see the degree of isolation between the different cytotypes.

The crosses generally comprised 10–15 flowers in each plant, which were all emasculated just before anthesis. All other flowers were removed. The shoot was isolated in a paper bag for some days. The seeds were germinated on moist filter paper (cf. p. 14) after rest during the winter.

The free pollination was, of course, of interest only for the allogamous species. The following clones were studied: tetraploid were four *R. sylvestris*, one *R. amphibia* and seven *R. amphibia* × *sylvestris* hybrids, pentaploid was one *R. sylvestris* and hexaploid four *R. sylvestris*. No diploids were available. This experiment would show which potentialities are present for out-breeding and seed-production in the self-incompatible clones under favourable conditions rarely met with in nature.

Table III combines the results obtained from the controlled crosses. There the yield of well-developed seeds and the number of germinated seeds are taken as measures of the success of the crosses. The seeds obtained in a cross were very unevenly distributed on the pollinated flowers, and as a rule some of those aborted totally. Since it cannot be decided how far damages during manipulations had caused failure of development, calculations of the mean number of seeds per pod

is of restricted significance. Moreover the number of ovules in the pods varies somewhat between the species (cf. Ch. 3).

The ratio of germinated seeds is mostly very low, rarely above 10 % and also those from crosses within a cytotype show low germination ratios. Only in a few cases did 25–50 % of the seeds germinate. As males plants with as good pollen as possible were chosen. The pollen quality is, however, often bad in *R. amphibia* and *R. sylvestris* (cf. pp. 87, 108). The low germination ratios are in contrast to the high ones found in seeds collected from spontaneous hybrid populations and from plants exposed to free pollination. The competition of pollen of various extraction may here partly account for the better seed quality.

In addition to the crosses listed in Table III I also tried to perform some back-crosses from artificial hybrids to one parent species. Seed-development was usually interrupted at an early stage and only very few good seeds developed, but they did not germinate. In contrast some spontaneous hybrids were easily crossed back to *R. amphibia*.

Yield of the crosses

Some remarks on single crosses in Table III will follow. On the tetraploid level it seems clear that crosses between *R. amphibia* and *R. palustris* or *R. sylvestris* are more successful than those between *R. palustris* and *R. sylvestris*. The latter crosses gave no progeny in spite of several attempts, made both as direct crosses and as isolations of intended parent plants.

It should be observed, too, that back-crosses of spontaneous *R. amphibia* hybrids to *R. amphibia* were successful, while attempts to cross *R. palustris* with *R. amphibia* × *sylvestris* hybrid gave only very few seeds. Also a tetraploid hybrid of *R. austriaca* × *sylvestris* when crossed back to tetraploid *R. sylvestris* gave rather rich progeny. Almost all controlled progeny from crosses at the tetraploid level had the number $2n=32$ (cf. Table III). As a rule both the pollen quality and the seed setting of the F_1 progeny are good. Left to free pollination well developed seeds were produced with few exceptions at a scale not much below that of the parent plants.

Crosses between different polyploidy levels were especially successful between tetra- and hexaploid *R. sylvestris* but also between tetraploid *R. amphibia* and hexaploid *R. sylvestris*. The seeds were here remarkably small but viable (cf. Howard & Manton 1946, Howard 1947*a*). Also here the F_1 plants were in general highly fertile, even those with aneuploid numbers. Also spontaneous tetraploid *R. amphibia* × *sylvestris* hybrids were successfully crossed with hexaploid *R. sylvestris*. On the other hand attempts to cross *R. palustris* with hexaploid *R. sylvestris* failed completely.

The pentaploid *Rorippa sylvestris* used in the crosses is J 357 throughout. Here, too, some progeny was obtained from crosses with *R. amphibia* × *sylvestris*

hybrids, while those with *R. palustris* failed. The F_1 progeny was of course here on the average less fertile and several totally barren plants were obtained.

Some crosses between diploids and tetraploids were also attempted. The failure to obtain progeny from the cross *R. islandica* × *palustris* (not in Table III) may be due to difficulties in handling these species. Reciprocal crosses between diploid and tetraploid *R. amphibia* gave in some cases plenty of seeds, none of which germinated. In some others an early interruption of seed-development was noticed. This also occurred in a cross between diploid *R. amphibia* and tetraploid *R. palustris*. Out of the crosses involving diploids those between *R. austriaca* and tetraploid *R. sylvestris* were successful, giving triploid progeny. *R. austriaca* crosses to its own tetraploid hybrid with *R. sylvestris*, to hexaploid *R. sylvestris* and to diploid *R. amphibia* failed totally.

The free pollination experiment clearly showed the facility of pentaploids to arise where tetra- and hexaploids are present. In fact, the majority of seedlings raised from hexaploid mother plants were pentaploid. Their formation was, however, favoured through the majority of tetraploids present and through the male sterility of two hexaploids. The latter circumstance certainly also contributes to the curious absence of hexaploids in the progeny, but a probable cause is also the frequent meiotic disturbances in all hexaploid *R. sylvestris* seen (cf. Table IV). Aneuploids were also frequent, and as expected they dominated the progeny of the pentaploid plant. But also seeds from tetra- and hexaploids gave rise to aneuploid plants, which indicates that the pollen from the pentaploid was effectively competing.

Properties of the progeny

In most F_1 generations a number of germlings died early (cf. Table III). Other germlings were very weak from the beginning but succeeded in forming the leaf-rosette of the first year (cf. p. 22). They later on formed floral shoots of normal vigour. Weak germlings are, as expected more frequent in aneuploid progeny. Weakness in this stage may be a primary cause of the absence of aneuploid plants in nature.

In both euploid and aneuploid progeny single luxuriant plants occurred, indicating "hybrid vigour" with respect to the size and branching of shoots.

The pollen of the aneuploid plants is of variable quality but many of them have grains of regular shape, up to 50 % of which stain in lactic blue. On this point the difference between aneuploid and euploid plants is not so manifest, since total or pronounced pollen sterility is not rare in euploid *R. sylvestris*. We evidently meet in these aneuploids a fairly high tolerance of genetic unbalance, whose effect is probably moderated through the rather high level of polyploidy. Similar good viability of aneuploid progeny was found in *Rorippa* sect. *Cardaminum* by Howard & Manton (1946). For cytological observations of the aneuploids see Ch. 2.

Table III. Survey of crossing experiments.

Crossing combinations (female × male)[a]	Numbers of crosses	Numbers of pollinated flowers	Numbers of well developed seeds	Numbers of germinated seeds	Numbers of progeny plants reaching flower	Chromosome numbers of the progeny[b]
R. amphibia (16)						
× R. amphibia (32)[c]	2	19	164	0	—	—
× R. palustris (32)	3	21	0	—	—	—
R. amphibia (32)						
× R. amphibia (16)	2	20	0	—	—	—
× R. amphibia (32)	1	10	29	1	—	—
× R. palustris (32)[d]	3	40	45	9	3	32
× R. sylvestris (32)	1	20	25	5	2	32
× R. sylvestris (40)	1	12	3	0	—	—
× R. sylvestris (48)	1	12	14	0	—	—
R. amph. × sylv. (32)						
× R. amphibia (16)	1	12	0	—	—	—
× R. amphibia (32)	4	44	225	72	20	32
× R. palustris (32)	2	24	8	0	—	—
× R. sylvestris (32)	1	11	153	0	—	—
× R. sylvestris (40)	3	34	177	7	4	38
× R. sylvestris (48)	3	31	89	3	3	32, 39, 40
R. austriaca (16)						
× R. amphibia (16)	1	10	14	—	—	—
× R. sylvestris (32)	1	10	36	5	0	(22), 24
× [R. austr. × sylv. (32)]	1	10	0	—	—	—
× R. sylvestris (48)	1	10	0	—	—	—
R. austr. × sylv. (32)						
× R. sylvestris (32)[e]	2	14	52	8	8	(31), 32
R. sylvestris (32)						
× R. austriaca (16)	1	10	0	—	—	—
× [R. austr. × sylv. (32)]	1	7	36	3	3	32
× R. amphibia (32)	3	27	171	5	4	32
× [R. amph. × sylv. (32)]	2	22	79	5	2	32
× R. palustris (32)[f]	9	87	12	1	0	—
× R. sylvestris (32)[g]	3	34	316	8	7	32
× R. sylvestris (40)	2	22	143	2	1	c. 32
× R. sylvestris (48)	3	34	325	12	11	40, (41)
R. sylvestris (40)						
× R. amphibia (16)	1	14	1	0	—	—
× R. amphibia (32)	1	12	35	0	—	—
× R. palustris (32)	1	11	0	—	—	—
× R. sylvestris (32)	1	10	34	2	2	—
× R. sylvestris (48)	1	15	107	16	12	36, 40, 41 43, 44

Crossing combinations (female × male)[a]	Numbers of crosses	Numbers of pollinated flowers	Numbers of well developed seeds	Numbers of germinated seeds	Numbers of progeny plants reaching flower	Chromosome numbers of the progeny[b]
R. sylvestris (48)						
× R. amphibia (16)	2	12	4	0	—	—
× R. amphibia (32)	2	24	126	40	32	(38, 39), 40
× R. palustris (32)[h]	2	25	0	—	—	—
× R. sylvestris (32)	2	25	379	16	9	(39), 40
× R. sylvestris (40)	2	23	226	24	14	38, 39, 40, 41, 44, 45, 47
× R. sylvestris (48)	4	49	269	15	10	48

[a] The somatic chromosome numbers are given within brackets.

[b] Chromosome numbers within brackets were found in a very small part of the progeny.

[c] All seeds from one cross.

[d] Small seeds.

[e] One cross successful, the other failed. The latter reciprocal of the successful one above.

[f] Seed development as a rule interrupted at an early stage.

[g] Plenty of seeds in 2 crosses, 19 in the third.

[h] Seed development interrupted at early stages.

Plants from the following collections were used for the crossings: J 143, 146, 171, 185, 186, 188, 252, 339, 344, 347, 351, 355, 357, 361, 364, 366, 367, 371, 372, 377, 379, 385, 387, 395, 401, 406, 409, 439, 441, 465, 471, 509, 514, 524, 531, 532, 539, 541, 573, 581, 870, 872, 890, 892, 900, 919, 940, 950, 955, 1074, 1077, 1112, 1123, 1271, 1572.

Well developed seeds were formed to a considerable degree in most pentaploids produced, irrespective of whether they were formed from crosses within *R. sylvestris* or between *R. amphibia* and *R. sylvestris*. Most of the pentaploids raised from free pollination had, to judge from their morphology, resulted from intraspecific *R. sylvestris* crosses and also set good seeds. Plants with aneuploid numbers showed only occasionally rich seed-production, e.g. some *R. amphibia* × *sylvestris* hybrids with $2n = 38$ and 39. In general very few seeds reached maturity in the aneuploids, and many of those plants seem totally unable to produce seeds. The chances for total sterility—and other aberrancies (see below)—seem to be about equal irrespective of what the exact chromosome number may be.

Morphological data of some of the artificial interspecific hybrids as compared to spontaneous ones is postponed to Ch. 6 (Table V). Here the variation range within F_1 progeny of different crosses will be presented. Only from few crosses were progeny of a size permitting comparisons raised. The crosses between *R.*

amphibia and *R. sylvestris* gave F_1 generations of highly constant and intermediate appearance. This is valid for the cross at tetraploid level as well as the one between the tetra- and hexaploid levels. In the latter cross no important dissimilarities were observed among the specimens, scarcely even in the aneuploid progeny. When the same *R. amphibia* plant (J 395)—also now as the male parent—was crossed with the tetraploid clones J 355 and J 372, a large number of forms segregated in the F_1. The variation of this progeny covered the range between the parents rather well, and there was, as expected, a close co-variation of parental characters in the progeny. This result confirms the hybrid nature of the clones J 355 and J 372 and indicates heterozygosis for lots of genes. It also points to the great possibilities of morphological variation that may appear from a single back-cross of a hybrid to one of its parent species. For partly other reasons great variation occurred in the progeny from crosses involving the pentaploid (J 357). Here supposed genetic unbalance of the resulting aneuploids might account for a variation sometimes approaching misformations. Besides floral organs leaf-shape seems to be particularly affected, resulting in narrow leaves with extremely narrow, completely entire segments. Such aberrants seem to arise in about equal frequency at any aneuploid number. In most cases, however, morphological variation of the aneuploids lies within the "normal" limits of the taxa concerned.

Genetic barriers

The results presented may permit some cautious statements on the genetic barriers operating between the species involved. On the tetraploid level only rather weak barriers seem to exist. *Rorippa amphibia* and *R. sylvestris* seem to be genetically very close to each other, while *R. palustris* is genetically perhaps more isolated. In nature the strong autogamy of *R. palustris* will certainly reinforce isolation against other species. Also between the tetra- and hexaploid levels the barriers are weak, as far as *R. amphibia* and *R. sylvestris* are concerned, which further indicates the close genetic relationship between the two. Through this combination as well as within *R. sylvestris* itself successful pentaploids could easily arise (cf. p. 126). Under favourable conditions subsequent formation of hybrid swarms including aneuploids is at least theoretically possible.

On the other hand rather strong barriers to gene exchange seem to exist between tetraploids and diploids, which is here exemplified by the failure of obtaining triploids within *R. amphibia*. The isolation between the levels is not absolute, since a completely sterile triploid hybrid between *Rorippa amphibia* and *R. palustris* is known (cf. Ch. 6 D), and since it was possible to cross diploid *R. austriaca* with tetraploid *R. sylvestris*. The latter circumstance together with the facility of forming fertile back-crosses on the tetraploid level (cf. above) point to a near relationship also between *R. austriaca* and *R. sylvestris*. This should make a close connex-

ion also between *R. austriaca* and *R. amphibia* plausible. The failure to cross these species at the diploid level is of little significance, since there are many examples of barriers existing between diploid cytotypes of two taxa, which break down between cytotypes on tetraploid or higher levels (Fagerlind 1937, Ehrendorfer 1959, 1965). No attempt to cross *R. amphibia* with the hybrid *R. austriaca* × *sylvestris* has hitherto been made.

VI. VARIATION, DISTRIBUTION AND TAXONOMY

A. The *Rorippa islandica* group

Differentiation between *Rorippa islandica* and *Rorippa palustris*

This account will supply evidence for the splitting of *R. islandica* s.lat. within Europe into two taxa of specific rank, the diploid *R. islandica* s.str. and the tetraploid *R. palustris*. Variation between and within the species will be treated, as well as distinguishing characters. The European populations will also be compared with those in Asia and America.

The *R. islandica* group has not been paid particular attention to by British and Nordic botanists, but has from special points of view been somewhat oftener dealt with in Central European (cf. p. 73) and especially North American taxonomic literature (cf. p. 74 f.). The slight interest for these plants might partly be due to their rather scattered and weedy occurrences, often sparse in individuals. Though by no means common except in restricted areas of the region, they have probably been regarded as rather trivial. In ecological and phytosociological literature they are hardly ever mentioned. Floristic and taxonomic authors have sometimes paid attention to divergent local populations or single specimens, also obvious modifications, and so a number of taxa of low rank have been described (e.g. by Beck 1890–93 and Rikli 1903. Cf. also Soó 1966). Among the infraspecific taxa some of those from the Alp region have a particular bearing upon the discussions about the discernment of the two species and will therefore be treated, while others will be totally left aside.

The treatment of the Eurasiatic populations as a single species was certainly promoted by the facility to delimit the *R. islandica* group from adjacent species. It is distinguished by a series of well-defined characters and hybrids with species outside the group are not easily formed in nature and have only local occurrences (cf. Ch. 8).

The two chromosome numbers known, diploid and tetraploid (cf. Ch. 2), provide a marked discontinuity within the *R. islandica* group. I have tried to find correlated discontinuities in the European material in other characters, particularly morphological ones.

Pollen. All normally developed specimens have good pollen. As a rule at least 90 % of the grains stain well in lactic blue (cf. p. 28). When grains from specimens with a known chromosome number are compared, a slight difference is found in average size between diploids and tetraploids (Table II), the equatorial diameters in the grains of the diploids being on the average 2–3 μ shorter than in those of the tetraploids. The pollen of the diploids is almost exclusively tricolpate, while in many tetraploids more than 50 % of the grains are tetracolpate (cf. p. 30).

Besides controlled diploids and tetraploids, Table II includes the pollen size of a number of specimens for which the chromosome number has not been checked. The *R. islandica* specimens fall almost entirely within the size range of the diploids, which is an indication of diploidy for them, too.

Seeds. Well developed seeds are mostly formed in great quantities. They vary a great deal both in shape, size and colour but especially the structure of the seed-coat proved to be of interest. Except in abnormal cases, this is always finely colliculate (cf. p. 34), but the size of the colliculi, each of which corresponds to an epidermal cell, varies markedly. To obtain a quantitative expression of this variation seeds from a number of specimens were sectioned (cf. p. 34). All diploid material available was exploited for this purpose and from the tetraploids samples were chosen in order to cover as much as possible of the gross morphological variation and geographical distribution. I also examined a number of herbarium specimens especially from Central Europe and Russia–W. Siberia.

The measurements comprised heights and widths of the epidermal cells, the latter dimension corresponding to the size of the colliculi. The heights were measured in sections at right angles to the seed surface, the widths in tangential sections (cf. Plate IV). In a diagram, Fig. 1, cell-widths are plotted against cell-heights. Thereby the material is divided on the whole into three swarms. The measures of single extreme cells of the extreme specimens in each swarm overlap but the plotted mean values of twenty measurements give clear separations. Two of the swarms have about the same range of cell width. All controlled diploids are included in the swarm with low and narrow cells. The third swarm is separated by having markedly wider cells and includes all the tetraploids. The two specimens (cell width c. 34 μ) that fall in the gap are from the Alps (cf. p. 61). The discontinuous variation in cell-height within plants with narrow cells is discussed in p. 64.

By inspection under a binocular lens a greater material was possible to assort into two groups with respect to roughness of the seed-coat. As far as European material is concerned there seems to be nearly discontinuous variation in this character.

Petals and sepals. The size variation of petals and sepals is considerable. In a diagram, Fig. 2 B, sepal length is plotted against petal length. As expected their

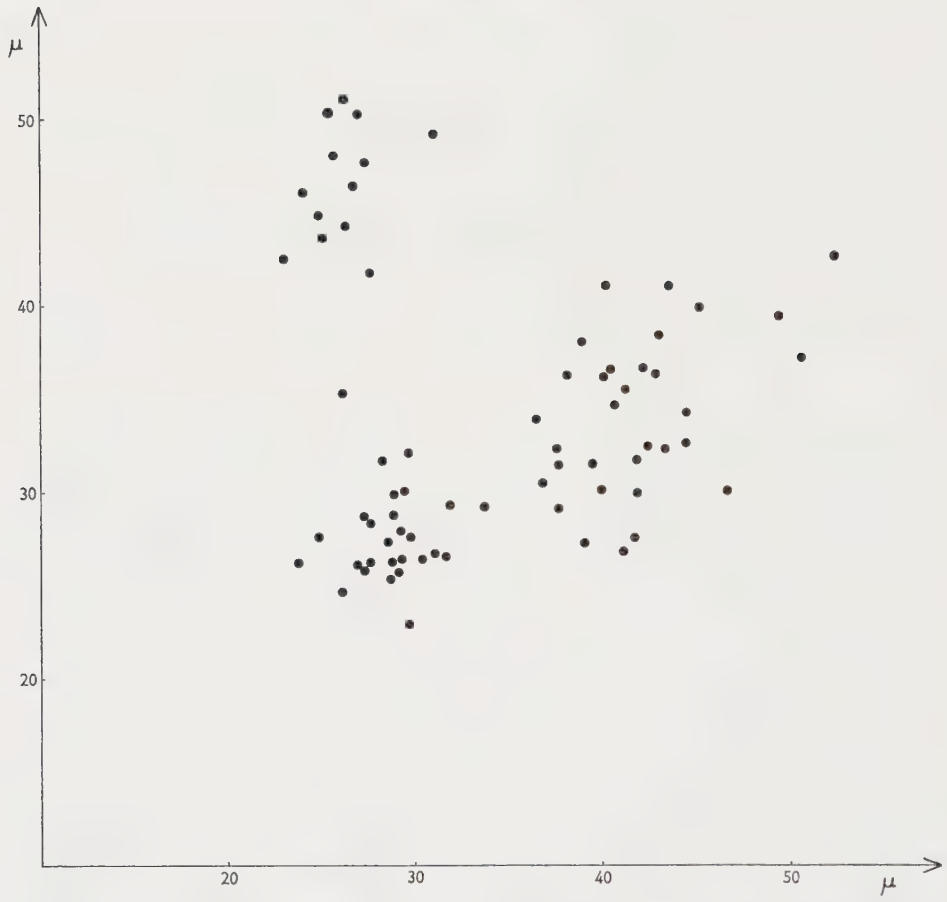

Fig. 1. *R. islandica* and *R. palustris*. Scatter diagram illustrating variation of *width* (horizontal axis) and *height* (vertical axis) *of cells of the outer seed epidermis* in European (and some Greenlandic and W. Siberian) material. Each symbol represents one herbarium collection and the mean value of 20 measurements of each variate.

variation is strongly correlated, the petals covering a somewhat wider range (from about 1.0 to 2.6 mm). The diagram only comprises specimens from N. W. Europe with a known chromosome number, and it is obvious that the two organs are shorter in the diploids. The cytotypes are nearly separated by the lengths of sepals. The mean values give some overlapping in the region 1.5–1.6 mm, and in single flowers the sepals may reach up to 1.7 mm in the diploids and down to 1.4 mm in the tetraploids. With respect to petal length there is a somewhat greater overlapping, since a few tetraploids (J 874, 876, 940) have poorly developed petals, but sepals of normal length. From the diagram it is also seen that the tetraploids have mostly proportionally somewhat longer petals than the diploids.

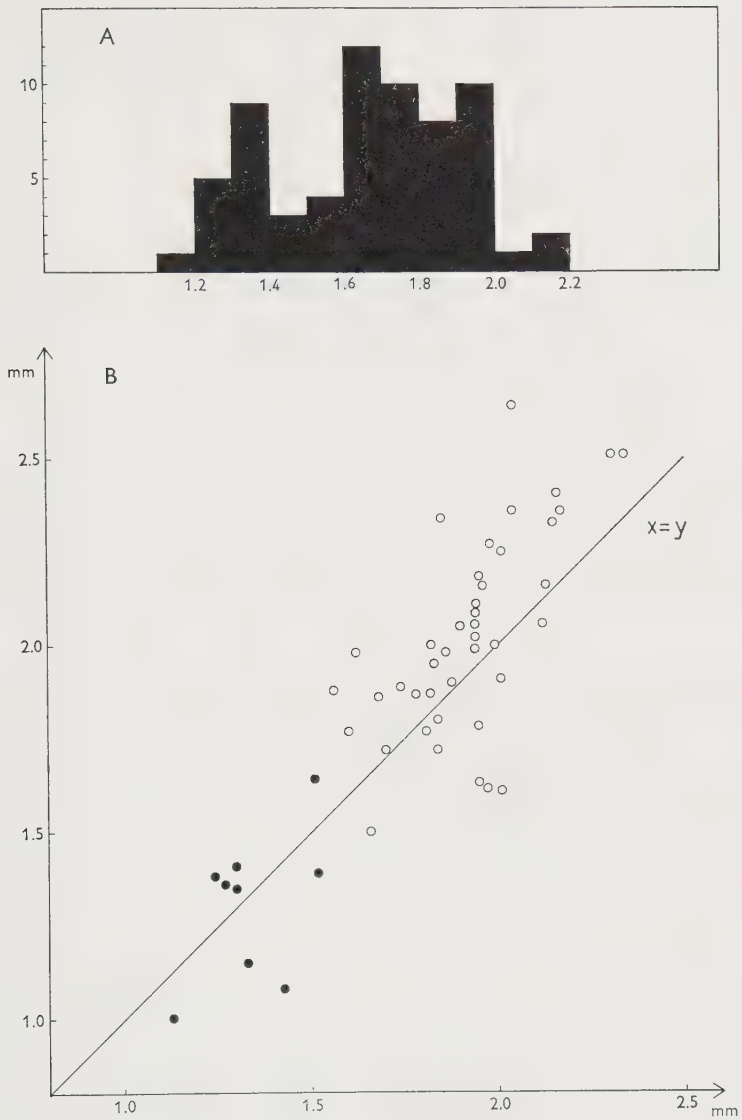

Fig. 2. *R. islandica* and *R. palustris*. Variation of flower-size in European material.

A. Histogram illustrating variation range of *sepal length* (horizontal axis) with numbers of collections indicated on vertical axis.

B. Scatter diagram illustrating correlated variation of *sepal length* (horizontal axis), *petal length* (vertical axis) and *chromosome number*. ● = diploids. ○ = tetraploids. Each symbol represents one collection and the mean value of 10 measurements of each variate. No collections are common to A and B.

The histogram (Fig. 2 A) is based upon herbarium material from various parts of Europe. The same variation range of the sepals is seen and there is a clear tendency to two frequency maxima corresponding to the controlled diploids and tetraploids in Fig. 2 B.

The width of the petals is also highly variable, but not always correlated with the length. The diploids have always narrow petals (up to 0.5 mm), but occasionally the longer petals of the tetraploids are only about 0.4–0.5 mm wide and even rolled up, compared to a normal width of 0.8–1.2 mm.

The smallness of the flowers in the diploid plants is a most conspicuous feature, brought still more into relief by the minute flowering racemes. It constitutes a distinctive character between the cytotypes, which is quantitatively best expressed by sepal length.

The two variates where discontinuities are most marked, namely width of seed epidermal cells and length of sepals, are plotted in another diagram, Fig. 3, which shows that the discontinuities are coincident. This is a strong indication that two taxa are present in the material. For reasons summarized in p. 55 they will be treated as two separate species: the diploid *R. islandica* with short sepals and a rather smooth seed-coat, and the tetraploid *R. palustris* with long sepals and a rather rough seed-coat.

Pods and pedicels. The shape of the ripe pods and their length in relation to the pedicels are the characters whose variation has been most frequently studied in European material of the *R. islandica* group. It is often commented upon on labels and sometimes in literature (Lange 1880, Norman 1894–95). The former author when working with J. M. Vahl's manuscript and material on Greenlandic plants, noted some divergent specimens of '*Nasturtium palustre*', which because of their long pods as compared to the pedicels were described as var. *longesiliquosa* (see also p. 58). The general variation on this point is illustrated in a pictorialized scatter diagram, Fig. 4. Both dimensions are evidently highly variable. But *R. islandica*, discerned in the diagram by the seed-coat character, has almost exclusively pedicels shorter than 4 mm (as mean value in a specimen), while those of *R. palustris* are normally longer. Single pedicels may, however, considerably exceed this limit in both directions. More constant in a specimen and therefore more useful as a key character is the ratio pod length/pedicel length. *R. islandica* has pods at least about twice the length of the pedicels, while those of *R. palustris* are not longer than twice the pedicels. There is some overlapping when the whole European material is considered, but all the same this character is among the best for determination work.

Further examination of the pods reveals some more discriminating characters difficult to express quantitatively. One is the shape of the base of the pod. In *R. palustris* the pod widens only gradually from the point of attachment, which

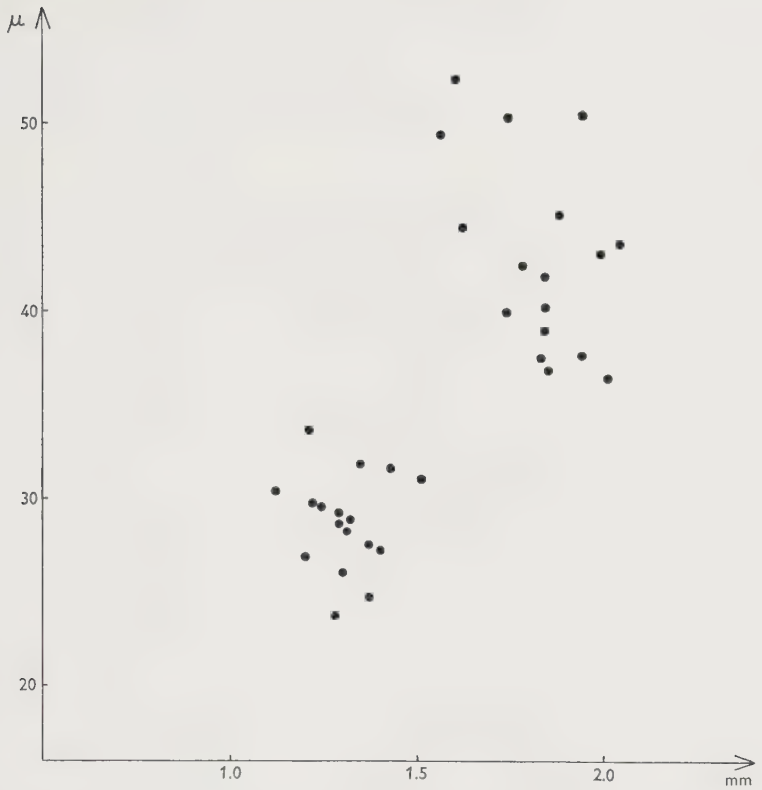

Fig. 3. *R. islandica* and *R. palustris*. Scatter diagram illustrating correlation between *sepal length* (horizontal axis) and *width of cells of the outer seed epidermis* (vertical axis). The diagram combines part of the data from Figs. 1 and 2.

means that the valves do not reach fully down to the pedicel, from which they are separated by a sterile portion of the pod like a short neck, usually c. 0.2–0.3 (0.5) mm. In *R. islandica* the pods widen more abruptly, and the valves reach down to the pedicel (neck not longer than c. 0.1 mm). This feature, easy to check in herbarium material, holds good with few exceptions (cf. Plate V, A–B).

When fully ripe the pods of *R. islandica* are often very large and have more rectangular valves than those of *R. palustris*. Young pods are often characteristically broader near the base, gradually tapering towards the style in a way rarely seen in *R. palustris* (Plate V, C-D). Moreover, and of greater importance, the valves of *R. islandica* look thin and transparent, those of *R. palustris* thicker and firmer. This depends on the existence in *R. palustris* of a layer of very small sclerenchymatous cells near the inner wall of the valves (Plate III, F–G). In *R. islandica* this layer is either totally absent or very incomplete. In the latter case portions of the

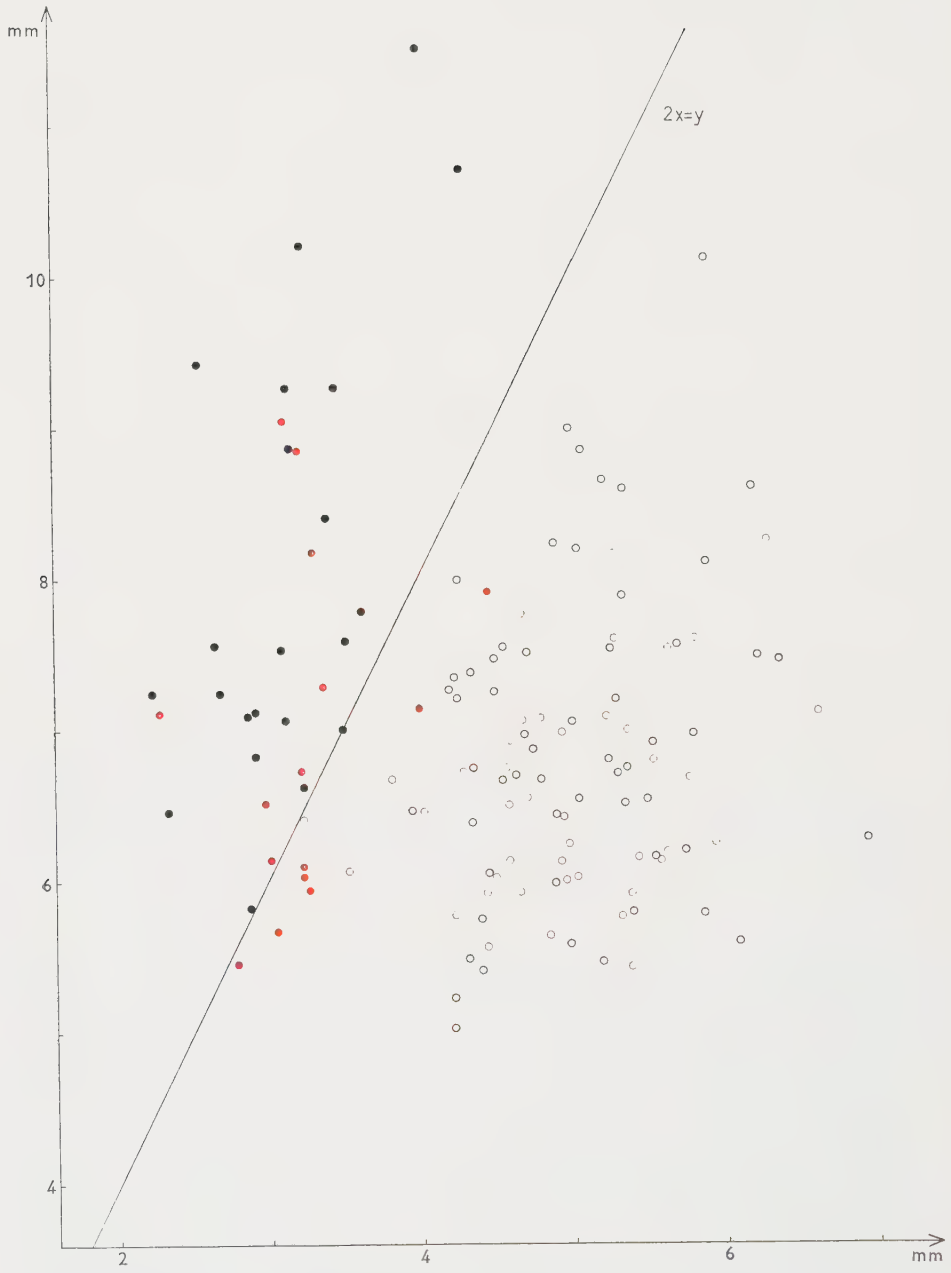

Fig. 4. *R. islandica* and *R. palustris*. Scatter diagram illustrating combined variation of *pod-length* (horizontal axis), *pedicel length* (vertical axis) and *seed-coat structure*. Filled symbols = fine seed-coat; open symbols = coarser seed-coat (cf. text). Black symbols = collections from N.W. Europe and Greenland; red symbols = collections from Central Europe. Each symbol represents one collection and the mean value of 10 measurements of each variate.

layer are found chiefly adjacent to vascular bundles and its cells are mostly not distinctly sclerenchymatous. The anatomical statements are based upon sections in about 70 European specimens. Further sections made in plants from other parts of the world, as well as external observation in most specimens seen provided additional support.

Foliage. Leaf-shape is a highly variable feature in the *R. islandica* group and is best observed in leaves from the middle part of the stem (cf. p. 24). They are always more or less lyrato-pinnatifid, but especially the size of the terminal lobe varies a lot, from very small ones to those stretching over half the leaf length, combined with a reduction in number of lateral segments from 6–7 pairs to one single pair or even none. From Fig. 5, A–H it is seen that *R. islandica* has on the whole narrow and numerous lateral segments together with a very small terminal lobe. The variation will be apparent from the series of corresponding leaves from both species represented in Fig. 5. The petioles are in *R. palustris* distinctly winged and mostly auriculate at their bases, which, in fact, make the leaves often appear sessile. *R. islandica* has petioles with inconspicuous wings and no auricles, and hence the leaves look stalked. Though more slender, the leaves of *R. islandica* are not unlike those of certain specimens of *R. sylvestris*, which at least in former times caused some confusion (cf. Oeder 1768, fasc. 7, p. 8).

Also in rosette leaves and in upper leaves supporting the racemes, corresponding differences prevail between the species. In *R. islandica* the rosette leaves are often more persisting throughout the season, a feature connected with its mode of growth (cf. below).

Branching and direction of stems. A most striking feature of *R. islandica* is its marked tendency to prostrate growth and branching from the base, while nearly all *R. palustris* examined have erect or at least rapidly ascending stems. This difference is obvious already in young plants. Seeds of *R. islandica* germinating in the greenhouse gave rise to plants ready to flower after about two months. Then two or three flowering shoots, surrounded by a leaf-rosette, have often been formed, branching up from just above the cotyledons. Those branches are initially directed upwards but are soon deflexed and continue growing almost horizontally. In vigorous plants the inflorescence is highly branched, but almost only in the horizontal plane and with the branches strongly divaricating from the main axis (Plate V D). *R. palustris*, on the contrary, forms only one erect shoot, branched only at some distance above the ground or not at all below the inflorescence. Branching from the base seems not to occur except until the second flowering season, when shoots are produced from the over-wintering buds (cf. p. 22). An exception I observed in living material of *R. palustris* from Alaska. Seedlings raised from the collection J 573 obtained prostrate shoots, but the plants were in

Fig. 5. Cauline leaves of *R. islandica* (A–H), *R. palustris* (I–Q) and *R. barbareifolia* (R–S). A–F: ssp. *islandica* (A: J 721. B and C: J 944. D: J 977. E: J 1055. F: J 1212). G–H: ssp. *dogadovae* (G: Poyarkov No. 280, LE. H: Dogadova & Tzvelev No. 852, isotype, BM). I–N: ssp. *palustris* (I: J 1079. J: J 499. K: J 957. L: J 364. M: J 1572. N: J 142). O: ssp. *fernaldiana* (J 1137). P–Q: ssp. *hispida* (P: 1892 Kennedy, GH. Q: 1923 Knowlton, GH). R–S: J 574. All leaves except C, P and Q from specimens in cultivation. $\frac{1}{2}$.

every other respect in complete agreement with *R. palustris*. Aberrant modes of growth observed in herbarium material may be only modifications.

In closing vegetation the decumbent growth manner of *R. islandica* sometimes seems to be prevented. The stem in such cases stands more or less erect, but is very slender and curved. The branching from the basal part is, however, usually still present.

The features found to separate *R. islandica* and *R. palustris* are partly of the kind often known to distinguish autopolyploids or near autopolyploids. Besides pollen size this may be valid for flower size and seed-coat structure. Though

Fig. 6. *R. islandica*. Flowering specimen with ripening pods. From a living plant (J 1046), c. 0.7 ×.

characters of this type are here of good use for a key, other differences e.g. in leaf-shape, pod-shape and mode of growth suggest at least partial dissimilarity of the genomes, and hence an allotetraploid origin of *R. palustris* with *R. islandica* as a possible component (cf. p. 85). Such a situation would warrant species rank of the two taxa. Their distribution patterns and to some extent ecology give additional support to this view, as well as the picture shown by the *R. islandica* group in the rest of the Holarctic region (cf. p. 84 f.). For nomenclatural discussions and typification see Ch. 7.

Rorippa islandica

From the map (Fig. 7) it is evident that *R. islandica* occurs in the European–North Atlantic region in three sharply distinct types of areas, Atlantic coast districts, Central European mountain districts and a Russian district, which reaches into Siberia and Kazakhstan. The Atlantic distribution, comprising parts of Iceland, Greenland, Norway and the British Isles will be treated first. Only from this area I had plants in cultivation. The localities from which the chromosome number $2n = 16$ has been determined are indicated in Fig. 7. My studies of

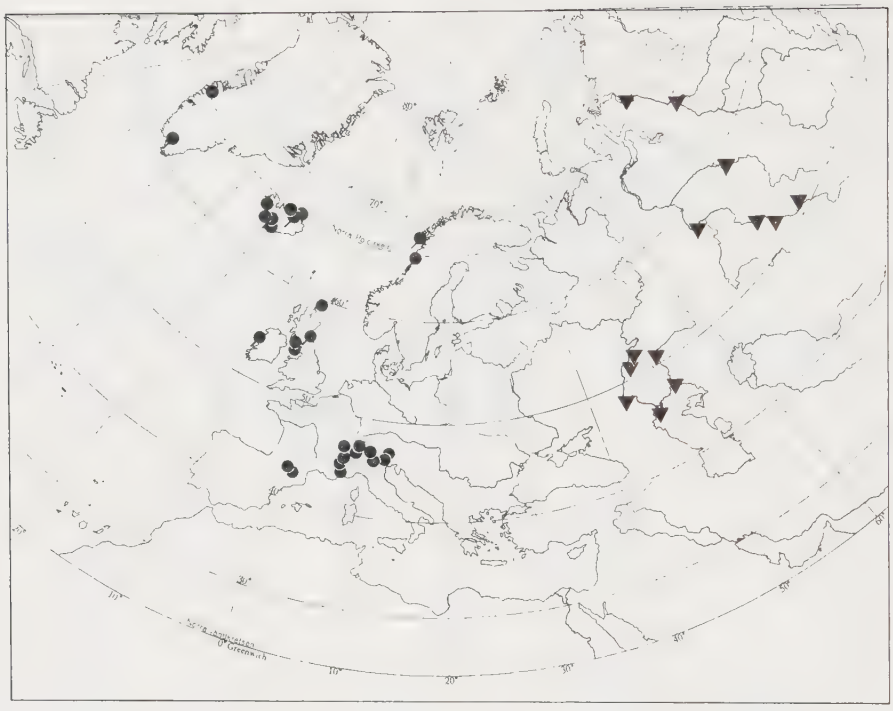

Fig. 7. Total distribution of *R. islandica* as documented by herbarium specimens. ● = ssp. *islandica*; ▼ = ssp. *dogadovae*. The oblique lines denote localities from which the chromosome number ($2n = 16$) has been verified. Many symbols, esp. in Iceland and the Alps, cover several localities close to each other.

Central European and Russian *R. islandica* were based entirely on herbarium material, and hence I am unfortunately unable to present any chromosome numbers from these areas.

The Atlantic distribution area

Though phenotypically variable the scattered Atlantic population seems highly uniform. I have only had a limited material (cf. App. 2) in cultivation but in that no variation of geographical significance has been noticed. Variation in the herbarium material as well can be estimated from Figs. 1–4.

The greatest number of localities in this area are known from Iceland, where the species occurs chiefly within two rather restricted regions: one northern (Eyjafjarðarsýsla—and Norður–Suður Thingeyjarsýsla with centre around L. Mývatn) and another in the large south-western lowland (centre in Árnessýsla). Besides that only scattered localities are known. The species is totally absent from

the eastern and north-western regions,[1] and also in all land above c. 300 m s.m., which excludes it from the whole inland part of Iceland (cf. App. 2 and map in Gröntved 1942). The densest population is perhaps that around Lake Mývatn. There I saw it growing abundantly on the narrow rim of lava gravel separating the water from the lava rocks along most parts of the lake. From here it has been extensively collected since the 1870-ies. In other Icelandic areas it seems to be a rare plant. It may occur at small bodies of water, on moist soil, also around farms etc. Oeder (1768) cited Koenig, who reported it from the surroundings of hot springs, a matter also mentioned by Gröntved (1942).

Examination of extensive collections from Scandinavia revealed only three specimens of *R. islandica*, all from Nordland fylke in Norway. One is from the Island of Væröy off Lofoten, collected by J. R. Landmark in 1898, the other two from some islands west and north-west of the Island of Dönna, by O. Dahl, who also published his finds (Dahl 1912). Landmark wrote on the label that the plant was growing "i mængde ved et tjærn i Nordlands udmark" (abundantly at a pool in the outlying land of [the village] Nordland). Exactly on the same place I found it growing in 1963 in thousands at the margins of four pools on clayey-sandy soil. The pools lie along a line of about 500 m on a strip of lowland, about 400 m broad. This strip constitutes a part of the northern coast of the island, and is separated from the sea by a sheltering natural wall. The soil is highly calcareous due to shell deposits, and the ground is grazed by cattle.

Dahl made his finds about 160 km further southwards, on the Island of Vandve, and in the Åsvær Archipelago. Vandve is a very flat island of 5.8 km² area. Dahl found the plant in a dried-out rock pool, but on my visit there in 1963 the species was not to be found in such a natural locality, but in a potato field, on grassy tramped soil and at a dry ditch, all within an area of 100 × 100 m. Perhaps extensive ditchings, which according to the inhabitants were performed after Dahl's visits, have destroyed the earlier localities. In the Åsvær Archipelago I found *R. islandica* on two small islands, Buröy (c. 700 × 300 m), where Dahl, too, saw it, and Risöy (c. 2000 × 400 m). In both cases it formed very small populations of less than 100 individuals restricted to an area of about 10–20 m². It grows on moist, loose, bare soil of very fine sand or clay surrounding rock pools only a few meters above sea level at flood tide, but which only very rarely would get an influx of sea-water. The growth place is obviously unstable with a sparse plant cover. Besides *R. islandica* such plants as *Ranunculus sceleratus* L. (a rare plant in this region), *Eleocharis uniglumis* (Link) Schult., *Agrostis stolonifera* L. and a sterile *Callitriche* grew on the place.

R. islandica was sought in vain in a number of adjacent islands, e.g. in Röst, the Gåsvær islets, and Dönna, where many suitable growth places seem to occur.

[1] In Stefánsson (1948) *R. islandica* was reported from Ísafjörður (N. W. Iceland), but I have found no collections from there.

Judging from the claims of rich soil typical for *Rorippa* species in general, *R. islandica* should not be expected to grow, however, on the bare soil at the numerous pools in the peaty inner parts, probably poorer of electrolytes, of most of those islands.

In the British Isles I have seen *R. islandica* growing in only one place: Renvyle, Connemara, W. Galway in Ireland. There it was collected in 1831 and 1832 (see App. 2) and was still growing in 1964. The population seen was very small: some tenths of individuals spread over about 10 m^2 of moist, bare soil. The locality is only about 50 m remote from the sea, and about 8 m s.m. The vegetation comprised in addition e.g. *Rorippa nasturtium-aquaticum* (L.) Hayek, *Potentilla anserina* L., *Cardamine pratensis* L. and *Ranunculus repens* L. A number of similar places at the Connemara coast were inspected with negative results. Perusal of British *Rorippa* material in a number of herbaria (see Ch. 1) gave only four more finds, three of which are from coastal districts, viz. from the Isle of Man, Wigtownshire and the Orkneys. The last find was published by Bennett (1909), but he did not detect any difference from *R. palustris*. The fourth British find is from a place about 20 km remote from the coast, marshes at the Threipmuir Reservoir, Pentland Hills, Midlothian in Scotland. In British county floras a few reports were found that may hint at *R. islandica* s.str. A constant occurrence (1813–1890-ies) at a small lake in Anglesey (Griffith 1895) may be this species. Scully (1916) reported from Co. Kerry (Ireland) about small prostrate forms growing on mud besides erect ones in other places. A record from the Shetlands (Druce 1925, cf. App. 3) is, however, *R. palustris*.

In the British Isles as well as in Scandinavia, *R. islandica* is consequently an extremely local and coast-bound plant, in sharp contrast to the much more widely distributed *R. palustris*. The two species have never been seen growing in the same place, not even in the vicinity of each other, nor are there any reports to indicate such a situation.

In Greenland *R. islandica* was first collected by J. M. Vahl in 1828 at the Tunugdliarfik firth in the southwest. These specimens were used by Lange (1880) to discern his variety *longesiliquosa* (cf. p. 50). From the same area the species has later been collected repeatedly in several places, lying at a maximal distance of only about 10 km from each other (App. 2). According to Lange (1880), Böcher (1938), Fredskild (1964 and in litt.) and to herbarium labels it grows at the margins of small lakes and temporary pools, as well as on or beside paths. *R. islandica* is present from one more Greenlandic locality about 130 km further northwards, at Söndre Strömfjord on the west coast (c. 66° N), where it was collected "at the margin of a small lake" by J. Jensen in 1884. Many Greenlandic specimens show, obviously phenotypically, a very compact growth with fruiting racemes shorter than the rosette leaves, suggesting severe conditions for the plant, at least during certain years.

From the locality descriptions given above one may conclude that *R. islandica* is ecologically close to *R. palustris* but shows much less weedy tendencies. In the vicinity of natural localities it may colonize soil laid bare by man at farms, roads, etc. This is the case in Greenland, Vandve in Norway and at Mývatn in Iceland. Not even in the last-mentioned region is it common as a weed, however, and *R. islandica* in Iceland shows no tendency to expand its area with modern communications, quite in contrast to the behaviour of *R. palustris* in North Fennoscandia (cf. below).

The map (Fig. 7) does certainly not give a complete picture of *R. islandica* in the Atlantic area, as the small, scattered and not always readily accessible populations easily escape detection. The species should be particularly looked for in Irish, Scottish and Norwegian coast districts, as well as in the Shetlands and the Faeroes. The recent thorough inventory of the last-mentioned archipelago has not yielded any finds of *R. islandica* (Hansen 1966). The main features of the map seem clear, however, and an attempt to interpret the distribution might be made.

Doubtless Iceland constitutes the present Atlantic centre of this species. Steindórsson (1962) regarded it as introduced to Iceland by man, but based his opinion partly on the assumed identity of the Icelandic plants with the widely distributed *R. palustris*. At the present stage it seems difficult to trace from where the plant should have arrived there, the more as the Atlantic distribution area is a fairly closed one, remote from at least plentiful occurrences. No conclusive arguments on the age of *R. islandica* in Iceland can be presented. According to certain theories on the climate of the last Ice Age (e.g. Böcher 1938) the species might well have endured. Others (e.g. Iversen 1952) do not suppose, however, that thermophilous plants had possibilities of surviving the conditions assumed to prevail close to glaciated areas. At least the northern of its two distribution centres coincides well with one of the most important possible refugia (around Eyjafjörður) supposed by a number of authors (Thórarinsson 1937, Steindórsson 1962, 1963, cf. also Lindroth 1963). Furthermore Steindórsson (1962) claimed a number of lowland species centering around the Eyjafjörður district to be survivors, all of which, however, belong to more stable plant communities than *R. islandica*. It was not considered improbable by Steindórsson (1962), however, that some aquatic lowland plants whose Icelandic distributions partly agree with *R. islandica* would be survivors. A probable survivor both in Iceland and Scandinavia, *Carex maclovіana* d'Urv., is at least in Lapponia lulensis almost exclusively occurring as an apophyte (Alm 1944, Selander 1950). It grows in Iceland in similar places namely pastures etc., and is on the whole confined to an area adjacent to the supposed Eyjafjörður refuge (Steindórsson 1962, 1963) and is extremely rare in the central highland of Iceland (Gröntved 1942). It does not exceed about 800 m s.m. in Scandinavia (Hultén 1950). The main objections to the view of *R. islandica* as a survivor of a glaciation in Iceland are still present, namely that it is here—but not

in Central Europe—a lowland species and that it rarely grows remote from human habitations, but judged from the presentation above they cannot be regarded indisputable. At any rate *R. islandica* is probably indigenous in Iceland, growing there since before man's arrival about 1100 years ago, but it might possibly have arrived with birds.

The distribution pattern of *R. islandica* in the Atlantic area is not exactly met among other plants, but approaches in many respects the picture displayed by the Icelandic plants assigned to the West-European–British element (Löve & Löve 1956). Among these are *Saxifraga hypnoides* L., *Thymus drucei* Ronn.; Jalas, *Sesleria coerulea* (L.) Ard. ssp. *calcarea* Hegi and *Ophioglossum azoricum* C. Presl, all with no or very few occurrences in Scandinavia, but with a much wider British distribution. For some of these plants a survival of the last Ice Age in Iceland was supposed (Löve & Löve 1956, Steindórsson 1962). Some members of the group are regarded to claim extreme oceanic conditions, e.g. *Saxifraga hypnoides* s.str. (Fægri 1960, Dupont 1962) but that seems not valid for *R. islandica*, since it grows in a Greenlandic region with a clearly continental climate (Böcher 1938), since it is not, like *S. hypnoides*, found in the euoceanic parts of Norway, and also because of its Central European occurrences (cf. p. 63).

For some other plants with a wide Icelandic distribution and a few Norwegian coast localities as *Thymus drucei* and *Galium normani* O. Dahl an anthropochorous transport from Iceland to Norway seems probable—it is just what must have happened in the direction from Europe to Iceland in a number of cases (cf. Steindórsson 1962). This hypothesis seems less probable for *R. islandica*, since it is known only from rather remote islands that would always have been off the tracks of communication and since in Iceland it is very rare at the coasts in contrast to the two plants cited, which grow plentifully practically everywhere, being two of the commonest and most abundant Icelandic plants.

The nature of the Norwegian localities makes it probable, however, that *R. islandica* has arrived there rather recently. Not only these localities but also most of those in the British Isles are situated on isolated islands or outer points of the mainland. The occurrence at pools on Grímsey north of Iceland (Jones 1934) is of the same type. To such places the species has probably been spread by migrating birds, which would regularly stop there after crossing the sea. Dispersal by geese across the Atlantic was discussed by Heslop-Harrison (1953) and Iversen (1952), and the general difficulties concerning theories of bird dispersal were outlined by D. Löve (1963). Dispersal in that way is imaginable for *R. islandica*, especially because a single seed under favourable circumstances could be enough to initiate a population of this autogamous species and because it is a colonizer of bare soil. It should be remembered, too, that the Mývatn district, where the densest occurrences of *R. islandica* have been found, is a region famous for its rich bird-life, especially waterfowl.

The Greenlandic occurrences may have another origin. All finds but one are in the vicinity of Qagssiarssuk, i.e. Brattahlíð, the centre of Norse colonization in the "Eystri byggd". There the species is obviously not uncommon, occurring in both more natural and in weedy localities. It is even reported close to Norse Ruins. Ostenfeld (1926) held the view that about 50 species, characterized by their distribution being mainly restricted to the two chief Norse settlement areas, were brought to Greenland by Norsemen. Ostenfeld's number was considered too high by M. P. Porsild (1932). *R. islandica*, however, is well connected to the group for which such an explanation seems possible, both with respect to Ostenfeld's criteria and two others set up by Porsild. One objection is, however, that it is a rather rare plant in Iceland, and not a plant of hayfields and meadows, although it may occur at farms.

Dispersal by birds must not, of course, be excluded in this case either, not least when the migration routes of Greenlandic geese mapped by Salomonsen (1950) (also in Iversen 1952) are considered.

It should be observed here that some Greenlandic finds referred to *R. islandica* s.lat. (e.g. Böcher 1938, A. E. Porsild 1945, Lagerkranz 1950, Pedersen 1965, Böcher, Holmen & Jacobsen 1966), do in fact refer to *R. palustris* (cf. App. 3).

The Central European distribution area

The richest Central European material of *R. islandica* emanates from the Alps. A few collections occur also from the Pyrenees (cf. Fig. 7 and App. 2). I am unable to see any important morphological differences between the Central-European (incl. Pyrenean) and the North Atlantic material. The Alp material has a slight tendency to shorter pods in relation to the pedicels (cf. Fig. 4), and to somewhat larger cells of the seed epidermis, which is in both cases a variation towards *R. palustris*. In other respects the variation lies within the same limits for both areas of the species. The limit towards *R. palustris* runs in fact sharply along nearly the same lines as in Scandinavia (cf. Fig. 4), and there seem to be also ecological differences between the two. The pollen size varies within the same range as for the North-Atlantic material (cf. Table II), which indicates diploidy in Central Europe, too.

The Alpine specimens range from Alpes-Maritimes in the south-west via Mont Cenis to Haute-Savoie and Valais, from where numerous records exist, and from there eastwards to Graubünden and Trentino–Alto Adige (cf. App. 2). No records were detected from the Northern Alps except one from Unterwalden. Altitudes given on the labels vary from about 1300 m to 2600 m, which centers around the forest limit (Schroeter 1908). The habitats mentioned are chiefly lake shores, sometimes said to be sandy–muddy. Calcareous soil is stated in some cases, siliquous in one case, and the species seems indifferent in this respect. No clearly apophytic occurrences were revealed, but it is unknown to what extent those cited

may be influenced by human activity. *R. islandica* seems doubtless to be indigenous in the region, but it should be expected to show hemerophilous tendencies. For the Pyrenean occurrences moist places and a pasture at 1800 m s.m. are reported.

The diverging appearance of the Alpine plant was first observed by Villars on specimens from small marshes close to the summit of Mt. Gondran near Briançon (Hautes-Alpes). Villars (1789, p. 341) gave a detailed description of the plant to which the name of *Sisymbrium pusillum* was applied by Villar (1785), already. He was, however, not convinced of its specific rank, nor to which species it would be most closely allied, giving both *Sisymbrium pyrenaicum* L. and a plant mentioned by Haller (1768) and Vaillant (1727) as possibilities. The former is rather obscure (cf. p. 150), the latter can be interpreted as *R. islandica* s.lat. A crude plate (Villars 1789 Plate 39) makes it still more clear that Villars's plant is an Alpine *R. islandica*. The original specimens for this plate were probably collected by Abbé Chaix, whose collection at Toulouse was destroyed in a fire (Timbal-Lagrave 1856, Breistroffer in litt.). De Candolle (1821) considered this plant to be only a variety of *Nasturtium palustre*. Later Rikli (1903) discussed *Sisymbrium pusillum*. He saw only a few specimens and did not decide about its taxonomic status. He commented, however, upon its mode of growth, leaf-shape and well developed pods and found all to be in contrast to the situation in the dwarf plants of other forms of *Nasturtium palustre* from corresponding altitudes. This evidently reflects an ecological difference between *R. palustris* and *R. islandica* in the Alp area. The former is a lowland plant, which sometimes ascends to altitudes where *R. islandica* normally thrives, but is then probably always as an apophyte and often small and more or less sterile.

A taxon erected by Brügger (1860), *Nasturtium palustre* DC. var. *montanum* is certainly identical with *R. islandica*. His descriptions of mode of growth and pod-length are especially characteristic and he pointed out how very dissimilar this plant is to the lowland *Nasturtium palustre*, which he called var. *erectum*. Furthermore the localities given seem typical for Alpine *R. islandica* (cf. App. 2). Only the first one he cited (Oberinnthal: dry road-sides at Landeck, alt. c. 900 m) is of a kind not otherwise met with, neither with respect to growth-place, nor to altitude. From one of the localities (Graubünden, Lenzerheide) a specimen collected by Brügger in 1849 exists (CHUR). Since it is not labelled as var. *montanum* I regard it as a lectotype. This plant, but no other form in the *R. islandica* complex, has been collected repeatedly in Lenzerheide. Also from other localities given by Brügger (op. cit.) there are a number of later *R. islandica* collections.

The Alpine *R. islandica* was once more described by Murr (1897) under the name *Nasturtium palustre* DC. var. *gelidum*. The identification is here made clear both by a rather detailed description and by a plate, which is simple, but shows the decicive features. It is furthermore confirmed by the fact that in a later paper

(Murr 1899) he assumed his own variety to be identical with var. *pusilla*. He believed (in Murr 1897) this plant to be the same "form" of *Nasturtium palustre* as that of northernmost Europe, which may indicate that he has seen specimens from Iceland. Murr's localities are given in App. 2.

Also some localities taken from Gelmi (1898, 1900) are included in App. 2, since this author under the name '*Rorippa palustris* Rchb. f. *pusilla* DC.' gave an unmistakable description as well as typical growth-places. In Rouy & Foucaud (1895), Dalla Torre & Sarnthein (1909) and Perrier de la Bathie (1917) some more records that probably concern *R. islandica*, but which I have not checked in herbaria, are found under the epithet '*pusilla*'.

The Alpine distribution of *R. islandica* coincides remarkably well with a number of regions considered by Braun-Blanquet (1924) to be especially rich in rare Alp species. These regions form a zone with some interruptions along the southern margin of the Alps from Alpes-Maritimes to Hohe Tauern in Austria. *R. islandica* is recorded for Mont Cenis, Zermatt, Ober-Engadin and the Dolomites among the regions mentioned by Braun-Blanquet, and from localities very close to some others. Somewhat remote from these stations are only the occurrences in Haute-Savoie, the northwestern parts of Valais, and the isolated find in Unterwalden. Braun-Blanquet claimed that these stations served as refugia at least during the last glaciation. The actual distribution pattern of *R. islandica* may thus indicate glacial survival.

On the other hand Braun-Blanquet (1924) pointed out that the western (Atlantic) element is extremely weakly represented in the Alp flora, and such species totally avoid this southern Alp margin. This supports the view held above that *R. islandica* is not a species bound to or specially favoured by oceanic conditions. The supposed refugia stations even coincide with the dry regions of the Central Alps (Braun-Blanquet op. cit.). Instead it seems reasonable to assume the species to have had before the last glaciation or earlier a much wider distribution in Central and Northern Europe. There can hardly be any edaphic or climatic factors preventing its occurrence over vast areas. Primarily owing to glaciations it would have become extinct except in restricted areas. The recent distribution may indicate a number of refugia districts for the species in West and Central Europe, one in the Alps, one in the Pyrenees and possibly one North-Atlantic. In the Atlantic area some post-glacial expansion has probably occurred (cf. p. 60). On the Alp populations nothing can be stated on this point. At any rate a post-glacial dispersal from the Alps to the Atlantic or vice versa seems highly improbable, since the species is evidently totally absent in the areas between.

The E. European–Asiatic distribution area

From single stations, chiefly at the borders of some large Russian and Siberian rivers specimens exist which come morphologically very near West and Central European *R. islandica*. I have seen collections from the rivers Volga, Ural, Ob,

Irtysh and Yenisey among others (see further App. 2). In a series of characters they agree with *R. islandica*, while they differ distinctly from *R. palustris*, also as this species is represented in Russia–Siberia. The main differentiating characters are the same as were displayed in Figs. 1–4 for *R. islandica v. R. palustris*. There seems also to be some constant differences towards typical *R. islandica*, particularly concerning foliage and seed epidermis. The leaves are more dissected, and there are often distinct secondary lobes, especially in the rosette leaves. The cells of the seed epidermis are narrow but very high, the average values being 42–52 μ against 36 μ as an isolated maximum in W. European *R. islandica* (Fig. 1, Plate IV). This exceeds even *R. palustris* where no averages higher than 44 μ were found (Fig. 1). Also the few North American specimens studied of taxa close to *R. islandica* have low cells in the seed epidermis.

This Russio-Siberian plant was described from near Pavlodar at the Irtysh in Kazakhstan by Tzvelev (1957) as *Rorippa dogadovae* n.sp., to which I, for reasons given below, will refer as *R. islandica* ssp. *dogadovae* (cf. also Ch. 8). Isotypes preserved in K, BM and S are among the material referred to above. Tzvelev described from living material the flowers as whitish, which means another difference against *R. islandica* impossible to check in herbaria after some years. He identified three other collections (all now in LE) with the new species. Having seen these specimens and checked their seed epidermis structure, I fully agree with this identification. They were collected at the River Aley (in Altay), at the Irtysh and at the Ural (cf. App. 2). According to Tzvelev (in litt.) the limit between *R. palustris* and *R. dogadovae* is sharp, also when they are growing together, which was the case at the Pavlodar locality.

From a Yenisey locality (Nikandrovskiy ostrov) *R. palustris* and—without being distinguished—*R. islandica* ssp. *dogadovae* were collected on the same occasion (1876 M. Brenner, H). The specimens fall within the normal variation range of each species and are consequently sharply distinguished from each other.

It would, however, have been surprising if this distinct, though not striking taxon had not been noticed at all by earlier Russian botanists. In fact it was obviously observed by Zinger (1885), who distinguished a taxon called *Nasturtium palustre β orientale*. I have not managed to find an authentic specimen. Zinger[1] noted as the differentiating characters of his plant the numerous prostrate floral shoots, which when the pods are ripe are still low enough to be concealed within the rosette leaves. This mode of growth is typical of *R. islandica* ssp. *islandica* under certain conditions and seems to be so also for ssp. *dogadovae* (e.g. the type collection). Zinger mentioned his plant only from the lower part of the R. Volga. From LE I have seen about ten collections from along the Volga, from south of

[1] I have not seen Zinger's work, but relevant parts were quoted to me by Dr N. Tzvelev from a copy at LE.

Kuibyshev down to the delta, which are quite in accordance with ssp. *dogadovae* even with respect to the seed epidermis. It seems therefore fairly safe to identify Zinger's *β orientale* with this species. Busch (1913–31) identified a few Siberian collections (all from Tobolsk at the Irtysh) with *β orientale*. I have seen only one of those (Mameev No. 162, K), and it is a typical ssp. *dogadovae*.

The known localities of ssp. *dogadovae* encircle a vast area of S.E. Russia, W. Siberia and a part of Central Asia, but the plant seems completely restricted to rivers with muddy shores. Along such rivers it can be suspected to be much more frequent than the few collections indicate.

Tzvelev (1957) compared in brief *R. dogadovae* with the North American species *Rorippa "obtusa"* (Nutt.) Britt., *R. lyrata* (Nutt.) Greene and *R. curvisiliqua* (Hook.) Bessey, to which he considered it to be closely related. This seems justifiable (cf. below) but after the discernment of *R. islandica* s.str. the morphological agreement with this one is still more striking, though there are the clear distinctions mentioned. Since this Russio-Siberian taxon is easily distinguished from the N. American taxa mentioned, but from *R. islandica* with certainty only after a study of the seed epidermal cells, I prefer to regard it as a subspecies. The formal combination is made in Ch. 8.

North American taxa close to Rorippa islandica

In North America and particularly in the western parts there are several taxa of the *R. islandica* group (cf. Ch. 1). Until recently they were very unsatisfactorily known and taxonomically confusing, but a study, still only partially published, was recently completed by Stuckey (1965, 1966*b*). His work means considerable changes of the traditional concepts, and a lot of nomenclatural alterations.

One of the species, now found to consist of several disparate elements (Stuckey 1966*b*) has usually been called *Rorippa obtusa* (Nutt.) Britt. in American handbooks. One of its components discerned by Stuckey is *R. curvipes* Greene, which I have in cultivation.[1] Since the name *R. obtusa* does not at all belong to a plant of this group (Stuckey 1966*b*), I will here refer to what was previously comprised by *R. obtusa* as the *R. curvipes* complex. In herbarium material referred to that group I have found several morphological agreements with *R. islandica*. On this point I have only investigated a limited amount of herbarium material, chiefly from K and BM, together with a few living plants (cf. App. 1). It is thus a preliminary study, which should be worth carrying through with revised American material.

R. islandica and the *R. curvipes* complex agree in having minute flowers and small seed epidermal cells, but also in more decisive features such as the prostrate-ascending growth, the mode of branching and especially the structure of the pod-valves, which in both are thin and devoid of the sclerenchymous layer described

[1] The cultivated material was kindly determined by R. Stuckey.

above (p. 51). Also the shape of the proximal end of the pods agrees with that of *R. islandica*. Also in western North America these characters seem to separate the *R. curvipes* complex from *R. palustris*, which is here very variable (cf. below). Stuckey (in litt.) reported that intermediate specimens are very rare. The picture is complicated, however, by species as *R. curvisiliqua* of the Pacific Coast region, which combines characters of the species mentioned.

To the *R. curvipes* complex belong some collections from the Mississippi River (state Missouri), by Stuckey attributed to a separate species, *R. truncata* (Jepson) Stuckey, which even as to shape of leaves and pods is close to *R. islandica*. The more dissected leaf-segments and the presence of auricles are the most apparent distinctions towards *R. islandica*, as judged from collections from St. Louis, Missouri (1845 Engelmann, K). Other taxa (mostly from the Rocky Mountain area) have the leaves more entire and the pods often rounded or short and pointed, but retain the general characters given above. The chromosome number $2n = 16$ was found in the cultivated *R. curvipes* plants (cf. Table I, App. 1). The connexion between the *R. curvipes* complex and *R. islandica* seems clear. Future studies might result in the view that some N. American taxon should be a subspecies of *R. islandica*.

From the Atlantic coast of North America I have seen only one collection morphologically approaching *R. islandica*, namely from Anticosti Island, Quebec, Canada (Marie-Victorin & Rolland-Germain No. 27265, GH, plate in Marie-Victorin 1930). Its habit, flower size and foliage suggest affinity to *R. islandica*. The leaflets are, however, more dissected and the petioles have distinct auricles at their bases. The pods (unripe in coll. cit.) show disagreements in a narrow style up to 1.2 mm long and probably in still other features. It seems clearly separate from *R. islandica*, reminding more of certain specimens of the *R. curvipes* complex, but a definite decision on this single specimen cannot be made. Fernald (1928) placed this very specimen in what he called the type variety of *R. islandica*, i.e. the European *R. palustris* (see further p. 76).

In p. 84 f. the distributional picture shown by *R. islandica* and some of the taxa close to it is discussed together with *R. palustris*.

Rorippa palustris

The distribution of *R. palustris* will not be discussed in detail (cf. p. 158). The maps in Hultén (1950) and Perring & Walters (1962) referred to *R. islandica* s.lat. would for relevant regions well represent *R. palustris* after exclusion of the localities for *R. islandica* given in App. 2 (cf. p. 56). For N. Norway, Scotland and Ireland more detailed information on the distribution of *R. palustris* is presented (cf. p. 71 and App. 3). Special attention was already above given to variation and occurrence of *R. palustris* in those Central European regions, where

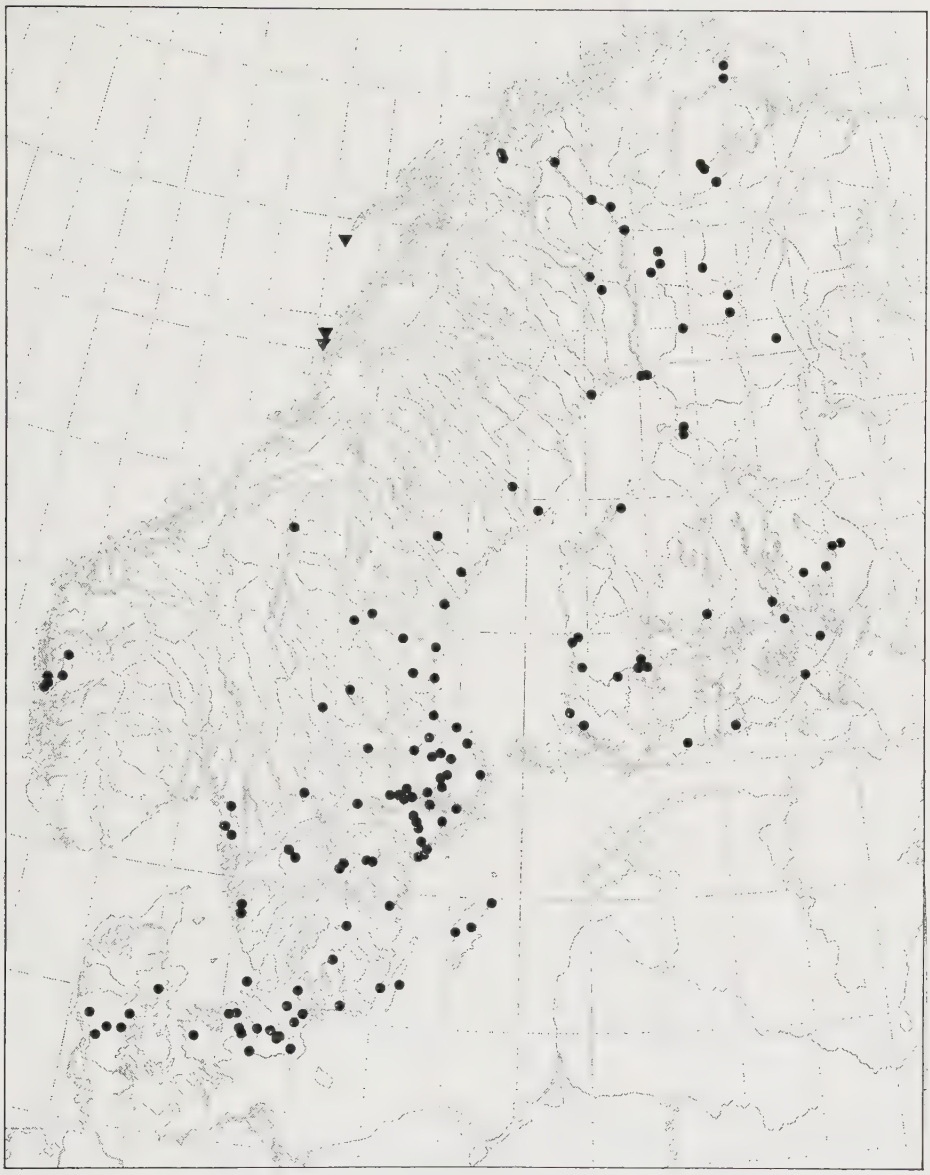

Fig. 8. *R. islandica* and *R. palustris*. Scandinavian localities from which chromosome numbers have been verified. ▼ = diploids (*R. islandica*); ● = tetraploids (*R. palustris*).

also *R. islandica* grows. The comments below will be made especially on Fennoscandian distribution in connexion with variation and ecology. From Iceland no specimen nor reports suggesting this species were seen, not even occurrences as ephemeral alien.

R. palustris, as circumscribed here, comprises so far only tetraploid plants, and is the only species in the *R. islandica* group known to be tetraploid. This conclusion is based at first hand upon counts of Nordic material (mapped in Fig. 8),but is supported by samples scattered over vast parts of the Holarctic range of the species, especially remaining parts of Europe and Canada.

Counted European material exists from the British Isles (J 1151, 1176, 1177, 1294, 1568, Howard 1947*c*), the Netherlands (J 1145), France (J 957, 1073, 1136, 1297), Germany (J 1134, 1298, 1461, 1468, 1586, 1591, Scheerer 1939), Switzerland (J 1566), Austria (J 1455), Czechoslovakia (J 954, 1470), Poland (J 1467) and U.S.S.R. (J 943, 1225, 1280). In two samples from the Asiatic part of U.S.S.R. I have counted the chromosomes (J 1075, 1539), and one determination has been reported from India (Raj 1965).

North American counts were made in material from Wisconsin (J 1137) and Alaska (J 573, 1573–1576, Mulligan 1964), but especially from Canada. My own and Mulligan's material represent together about 15 localities from Nova Scotia, Quebec (J 1285), Ontario, Manitoba, Saskatchewan (J 1472, 1473, 1477), Alberta (J 1282), Brit. Columbia, Mackenzie Terr. (J 1452, 1453) and Yukon Terr. They cover rather much of the morphological variation and include material of all the subspecies (cf. Ch. 8) except the Pacific ssp. *occidentalis*.

The general pattern of genotypical variation in *Rorippa palustris*, is dependent upon the strong autogamy. As discussed in Ch. 4 this should favour the establishment of fairly homogeneous local populations, which may, however, appear extreme in one character or another. A few examples will be given below.

Pod-shape has most often been taken as the basic criterion for taxa of infraspecific rank (e.g. Regel 1861, Beck 1890–93, Rouy & Foucaud 1895). Within Europe there is actually a conspicuous genotypic variation (cf. p. 33) on this point. To begin with the situation in Nordic material in this and other respects will be discussed.

Rorippa palustris in the Nordic area

Morphological variation. The three scatter diagrams Fig. 9, B–D show the variation amplitude of pod-size and pod-shape for each of three zones across Fennoscandia and Denmark, the latitudes 60° N and 65° N being arbitrarily taken as borderlines. The zones will be referred to as Southern Scandinavia, Central and Northern Fennoscandia. There are obvious differences in the variation pattern of pod-size between each of these zones, which is best observed in the length/width ratio. In Southern Scandinavia pod-length is on the whole about three to just four times

the width. Only single specimens fall outside the main group. In Northern Fennoscandia pods with a length about two–three times the width are common, but the variation seems to be greater than in Southern Scandinavia. In the intermediate zone, Central Fennoscandia, the variation is largest, since specimens occur in about equal frequency with pod-length about two–four times the width.

Variation of leaf-shape is also included in Fig. 9. It is expressed as the average number of pairs of lateral segments in cauline leaves, and the material is according to that character divided into five classes (cf. Fig. 5 and Ch. 3). In Southern Scandinavia the cauline leaves have three or more pairs of lateral segments, while in Central and Northern Fennoscandia leaves with fewer pairs of segments occur in many specimens. Outstanding in the northern material are the specimens that have both very few pairs of leaf segments and short, stout pods. They will be further discussed in pp. 70–72. Leaf-shape also comprises e.g. denticulation of single segments and size of auricles, but variation on these points seems to occur more at random in the Fennoscandian material.

Other features showing more notable variation in Nordic material of *R. palustris* are size of petals and sepals, style-length, plant-height, branching and perennity. The variation of the first-mentioned organs can be estimated from Fig. 2. This variation appears to be distributed more at random. Large flowers (petals c. 2.5 mm, sepals 2.1–2.4 mm) characterize, however, many northern specimens. Since pods and flowers are not generally found in the same herbarium specimen, the degree of correlation in the variation of these characters is difficult to estimate. The greater variability in N. Fennoscandia will below be seen in relation to ecology and dispersal of the species in that region. Style-lengths in ripe pods vary from mean values of about 0.4–1.1 mm, but no correlation was observed with variation in other respects.

Plant-height and branching are features obviously closely connected. On this point the genotypic variation is in nature covered by the phenotypic (cf. p. 22) and can therefore only be evaluated in cultivated plants. Erect, stiff and sparsely branched plants are found especially in the North Fennoscandian material. Striking is also a form on sea-wrack (J 1084), which only formed a leaf-rosette and c. 10 cm high erect stems. In herbaria other sea-wrack collections of similar appearance were seen, but they may be only modifications. In the Nordic material no prostrate-decumbent forms, known from other regions (e.g. Alaska: J 573) were discovered.

Plants or populations that are extreme in one character or another occur, as it seems, scattered at random over the region. Such deviating populations may be a result of homozygosis, of introduction from other regions, or of a combination of both. In the Jyväskylä region (Tavastia borealis, Finland), for instance, a local population occurs, which deviates by small, ellipsoid pods (e.g. 1916 Linkola, 1939 Lehtonen, 1953 Valovirta, all H) and similar plants have been collected in Sortavala (Karelia ladogensis, Finland; 1902 Vartiainen and 1927 Saxén, both H).

Ecology and dispersal, especially in N. Fennoscandia. In the mesotrophic-eutrophic cultivated parts of Fennoscandia where *R. palustris* is a regular but often sparse plant, it seems to be indigenous though strongly apophytic. From more natural localities (sandy-clayey lake and river banks) it spreads to ditches, moist tramped paddocks etc. As mentioned above it sometimes occurs on sea-wrack, especially at the Baltic (cf. Wahlenberg 1824, Sterner 1938, Englund 1942, Skult 1961). More rarely it appears as a weed of arable fields, along roadsides and railways or on other fairly dry localities. In Öland (Sweden), for example, it is not uncommon on sea-wrack but has only to a very small extent been found apophytically in the inland parts (Sterner 1938), probably due to lack of suitable moisture.

In the northern parts of Fennoscandia the situation is in many respects different. Occurrences of a natural character are mainly alluvial, sometimes at lakes, on sandy or gravelly banks. Several authors (Hjelt 1904–06, Cajander 1909, Dahl 1934, Benum 1958) have regarded *R. palustris* indigenous in such localities in Northern Norway and Finland, but it was always considered rare and even ephemeral (Norman 1894–95). The fact that plants combining very short pods and large terminal leaf-segments (cf. p. 69) are found in many of these localities, and nearly only there, support the assumption of their indigenity. The circumstances that *R. palustris* from the North seems to perennate better than plants of southern origin and that in the experimental garden many of the northern specimens begin to flower before the Central and South Scandinavian ones point the same way.

Specimens with short, stout pods, large terminal leaf-segments and long petals (cf. p. 69) are found as most typical at rivers in the Kola peninsula and westwards through Lapponia Imandrae and petsamoënsis to Finnmark (especially at Tana River, the northernmost occurrences known in Europe), and though less pronounced, to Troms. Also the Kuusamo region harbours populations of this type. Also in Finnish Lapland and along the rivers of Northern Sweden similar but mostly less typical populations occur, e.g. from the systems of the rivers Torne älv (J 1118, 1572), Kalix älv (J 938, 942), Ångermanälven (J 142, 1456), Ljusnan (J 169, 1117) and, furthest to the south, Dalälven (J 1079, but not J 946). Herbarium specimens of this type exist from still more water-systems.

Many specimens from lakes and rivers of Northern Fennoscandia, also those collected in former times (i.e. before 1900) agree, however, in most respects with South Fennoscandian *Rorippa palustris* (cf. Fig. 9). They make an indigenous impression but might as well be naturalized anthropochores of former times, when suitable habitats other than shores were rare in those districts.

The river and lake populations of course often grow apophytically e.g. at bridges, embankments, floating timber. In Northern Fennoscandia, however, *R. palustris* is nowadays most common as a real weed, often growing far from water-bodies. The spread of *R. palustris* as a weed is in these regions naturally tied up with the break-through of modern communications, which is also seen from the fact that

Hjelt (1904–06) mentioned only one case of clear hemerophily for this species in Lapland (at Lake Inari), and since hardly any herbarium specimens collected before 1900 give evidence of having grown as weeds. At railway stations this lowland species reaches its highest altitudes (Storlien, Jämtland 593 m s.m., Vassijaure, Lapponia tornensis 513 m s.m.; altitudes acc. to Arell 1915). As judged from my own observations especially in Finnish Lapland, the species is now often found in places far from habitats of spontaneous character. It is a regular, but not abundant, colonizer along the expanding net of roads. It grows here often in surprisingly dry spots and is often sparsely branched, erect and strikingly anthocyanic. Simmons (1910) discussed such plants from the Kiruna region (Lapponia tornensis) and considered them as recently introduced, which seems highly plausible since *R. palustris* is recorded from many places along the railway Luleå–Narvik (cf. Almquist 1957). Simmons (op. cit.) identified the plants with var. *erectum* Brügger from Central Europe, which is, in fact, only a name for *R. palustris* s.str. in contrast to *R. islandica* (cf. p. 62).

Over vast regions *R. palustris* should now be characterized as an anthropochore rather than an apophyte, though it is difficult to establish whether the colonizer is an alien element or emanates from natural populations of the North. Linkola (1916, 1921) regarded populations of similar growth-places in the Karelian inland north of Lake Ladoga as anthropochorous, in contrast to the apophytic populations, which he recorded from the Ladoga district, where he considered the species to be indigenous along some shores of lakes and rivers. At any rate weeds showing the characters of the alluvial plants from the extreme North (Finnmark–Kola), are rare. One case was recorded from Banak, Finnmark after the second World War (cf. App. 3), but in Finnmark *R. palustris* has not spread markedly as a weed.

Except in N. Finland and N. Sweden *R. palustris* is now expanding as a weed also in Norway, particularly in the region from Hordaland to southern Troms, according to available herbarium material. According to a map in Flora Murmansk. Obl. (1956) the species seems to be widespread also around the industrial districts of the Kola peninsula, which indicates a recent colonizing there, too. On the same map the alluvial localities known especially from specimens in Finnish herbaria (App. 3) are omitted, and hence it gives a rather misleading total picture.

The map in Hultén (1950) gives partly a picture of the distribution in the northern parts of Fennoscandia that is no longer actual. For the rest of the Scandinavian countries the species is in most handbooks considered as fairly common, which is on the whole correct as a general statement. Seen in details, however, the distribution is there very scattered and the species is seldom abundant, as is evident from detail maps (see Ch. 8) and local flora lists.

The above account has shown that the variation pattern displayed by *R. palustris* in Fennoscandia is rather complex, being probably the result of historic and recent dispersal within the region *inter alia*. As to the obviously indigenous north-

ern populations mentioned their morphology and ecology clearly suggest them to have another history than the rest of Fennoscandian *R. palustris*. It seems reasonable to suppose an immigration from north-east for this northern, primarily alluvial population. Kalela (1943) discussed the alluvial flora of North Russia and Siberia, the characteristic species of which in general do not reach Fennoscandia. Some species, particularly those with weedy tendencies, should in spite of the scarcity of typical alluvial habitats have advanced further westwards, to the westernmost coastland of the White Sea (Kantalahti), and from there either continued in a south-western direction via Kuusamo, or in a north-western towards and along the coast of the Arctic Sea. The northern *R. palustris* seems to fit this picture fairly well, since it is most typical in Finnmark, Lapponia petsamoënsis and the Kola region on the one hand and the Kuusamo region on the other. Very little material from North Russia was available for examination, but specimens corresponding to the actual form occur from the Dvina River. The populations of Fennoscandian rivers and lakes further west and south, which show similar though less extreme features may have arisen from an amalgamation of the north-eastern and southern populations.

A similar case was demonstrated by Ahti (1962) for *Erysimum cheiranthoides* L. which in Fennoscandia comprises a north-eastern population, ecologically specialized, and a much more widespread southern one, the common weed. In this case there are, however, clear distinctions between the two populations meriting their treatment as subspecies, while for *Rorippa palustris* a taxonomic subdivision of the Fennoscandian population is not justified (cf. p. 83).

Rorippa palustris in the rest of Europe

R. palustris is all over Europe except for the Mediterranean region a rather common lowland plant. Its altitudinal limit is difficult to establish since it is evidently taken as an anthropochore to altitudes where it does not normally thrive (cf. pp. 61–62). I have, however, not seen Alp material collected above 1800 m (cf. App. 3). *R. palustris* in the extra-Nordic parts of Europe was studied by me with the main intention of demonstrating a clear distinction between this species and *R. islandica* (cf. p. 50). Variation within *R. palustris* was regarded to be of secondary importance, not least as indigenous and introduced populations can nowhere be separated from each other. The material cultivated by me is also insufficient. Some observations may nevertheless be worth recording. *R. palustris* is fairly uniform (Fig. 9 A) all over Europe. The pods are usually 2.5–4 times as long as wide, the pedicels horizontal or deflexed, the cauline leaves on the average with 3–5 pairs of lateral segments and a terminal one of about one third of the total leaf-length. In these features the variation range is about the same as in the South Scandinavian populations.

Most *formae* described from Central Europe are probably only modifications and,

in a few cases, abnormities (cf. e.g. Beck 1890–93, Rikli 1903, Soó 1966). The variation towards short and stout pods, which occur but are rare would, however, here as well as in Scandinavia be genotypic. To such a form from Austria Beck (op. cit.) gave the name *R. palustris β microcarpa*. Under that name also a number of similar plants from the British Isles have been reported (Britton 1920, Druce 1928). This pod-shape does not here seem to be correlated with any other divergent features and is hence of little importance. Some taxa of low rank as var. *erectum* Brügger (1860) were described in contrast to what is now discerned as *R. islandica*.

To a small extent N. American forms have probably been introduced to Europe, as exemplified by a specimen from Cardiff, Wales (NMW 30 · 33 · 26) that has short, rounded pods and dense pubescence on the stem and the lower sides of the leaves.

In App. 3 I have listed specimens of *R. palustris* from Scotland and Ireland, the Alp and Pyrenean regions in order to outline the distribution of this species in contrast to *R. islandica*. Moreover all Welsh specimens enumerated under *R. islandica* s.lat. in Hyde & Wade (1957) belong to *R. palustris*. Collections of *R. palustris* in some widespread European exsiccata are also included in App. 3.

Rorippa palustris outside Europe

General distribution. R. palustris has a nearly complete circumpolar distribution. Hultén (1937*b*) recorded distributional gaps from Greenland and the Bering Sea area. The first one holds well, since it is in Greenland recently introduced, but the second is on the whole filled up already through the statements by Hultén (1945). From the evidence presented here it follows that Iceland constitutes an additional gap.

R. palustris seems nowhere to reach the Arctic zone as circumscribed e.g. by Polunin (1959), except as an anthropochore as in Greenland. There it grows, contrasting *R. islandica* (cf. p. 61), as a weed, and is known only from the Ivigtut area where it is now widespread (A. E. Porsild 1945, Pedersen 1965, cf. App. 3). Occurrences reported by Polunin (1959) from Arctic Siberia are most likely recent introductions, as are certainly the finds on the Arctic Slope of Alaska (e.g. J 573).

South of the Holarctic range the differences between spontaneous and anthropochorous distribution are still more indistinct. There are plenty of specimens from Japan and China, and like many Holarctic plants *R. palustris* occurs in the Himalayan region as well as in the Central Asiatic mountain areas and in the Caucasus (J 1075). In these areas the species is doubtless indigenous. In the Mediterranean region it is very rare and probably introduced perhaps with the exception of some occurrences in the mountains of the northern Mediterranean area. From North America it reaches down to Central America and the West Indies. In the rest of the world it is probably only introduced (cf. p. 158).

The following account will treat of a part of the Holarctic area. It aims at putting

the European material in relation to the Holarctic variation pattern and is therefore restricted to a few problems. As emphasized above *R. palustris* seems distinctly separate from *R. islandica* and taxa close to this species even in western North America, where diversity is most intense in *R. palustris*, too (cf. p. 85). Studying *R. palustris* specimens from circumpolar regions one is struck by the much greater variability displayed in North America and to some extent East Siberia. Variation there goes beyond that found in other Asiatic and in European material in diverse features, but especially striking are the occurrences of a rich indumentum in stalk and leaves, of very tall and robust specimens, of leaves with acutely angular segments and of spheroid pods. Before a comparison of this variation with the European one, I shall give a critical survey of the taxonomic treatment of *R. palustris* in the Holarctic, as far as it has bearing upon the following discussion.

Some extra-European taxa. Among the many taxa described within extra-European populations of *R. palustris* only a few, which are of special interest in the following, will be presented. They are all connected with the taxonomy of *R. palustris* in N. E. America.

Desvaux (1814) described the species *Brachilobos hispidus* on material in P. de Beauvois's herbarium obviously collected in Pennsylvania. Desvaux did not compare his new species with any previously known, but gave *inter alia* the following characteristics: stalk very tall, branched, villous-tomentose, leaves somewhat villous, pods short ellipsoid. During the 19th century this taxon was mostly given infraspecific rank under *R. palustris*.

Fernald (1928) regarded the European and N. E. American populations of *R. palustris* to be separate on at least a varietal (i.e. subspecific;[1] cf. Clausen 1941), perhaps a specific level. He initially gave the N. American population specific rank, *Rorippa hispida* (Desv.) Britton, with a var. *glabrata* Lunell comprising the more or less glabrous material. He regarded this variable species as distributed from N. E. America westwards to Japan. This wide circumscription of *R. hispida* was soon abandoned, and the name was again used only for material more close to Desvaux's description. In a restricted sense (though incl. *R. barbareifolia*, cf. p. 85) *R. hispida* was maintained as a species by Hultén (1945). Butters & Abbe (1940) and now also Fernald (1940) recognized the taxon only as a variety, *R. islandica* s.lat. var. *hispida* (Desv.) Butters & Abbe. From the series of diagrams (Fig. 9, E–H), which are more fully discussed in p. 80, some important characters of this taxon can be assessed. Particularly from Fig. 9 E, a marked correlation can be noted between pod-shape and pubescence: specimens with proportionately short pods have also a strong pubescence. These specimens have in general also a

[1] Var. *hispida* and var. *fernaldiana* (cf. below) will here be referred to as subspecies. The formal combinations under *R. palustris* are made in Ch. 8.

special leaf-shape, where the number of lateral segments is 4–6, against 2–3 in much of the rest of the material. The leaves have rather acutely angled lobes, and especially the terminal segment has often a rhomboid shape (see Fig. 5, P–Q). By these characters a ssp. *hispida* would be fairly well distinguished. But in spite of the rather strong correlation between the features mentioned there seems to be no discontinuous variation of any character that could separate these plants from the rest of *R. palustris*. Intermediaries showing a rich pattern of various character combinations are frequent, and occur scattered over most of northern N. America. Typical ssp. *hispida* occurs on the whole sympatrically with other forms of the species at least in Central and Eastern Canada. All Siberian material attributed to this taxon seems to be *R. barbareifolia*. From natural occurrences at lakes and rivers it has obviously spread widely as a weed. It is very plausible that the possibilities for spread as weeds opened for American *R. palustris* has contributed to render more diffuse such distinctions which may have existed in both morphology and distribution pattern.

The part of N. E. American *R. palustris* falling outside ssp. *hispida* in narrow sense (*R. hispida* var. *glabrata* Lunell s. Fernald 1928) came to be regarded as another variety of *R. islandica* s.lat. Since Butters & Abbe (1940) did not regard the type of var. *glabrata* (from Idaho) to fall within the actual N. E. American taxon, they made for that a new name, *R. islandica* var. *fernaldiana*, the type of which is a specimen from Maine (cf. Ch. 8). Butters & Abbe (op. cit.) claimed the shapes of pods and stigmata to be of special importance as separating this taxon from the European one. The length/width ratio of the pods was given as on the average 2.6 (extremes 2.0–3.4) in var. *fernaldiana* against 3.6 (3.1–5.5) in European plants. The stigmata should be only sub-capitate in the former, but distinctly capitate and usually 0.1 mm wider than the upper end of the style in the latter case. To these statements I shall return in p. 81. For pod-width Butters & Abbe (op. cit.) gave a mean value in var. *fernaldiana* as low as 1.6 mm (lowest extreme 1.2 mm), while in ripe pods of American plants I have not measured widths below 1.7 mm. It is also apparent that both the holotype and the isotype photographed in Fernald (1940) have completely unripe pods. Pod-width does therefore not distingush var. *fernaldiana* from other varieties of the species as well as would be imagined from the description. Butters & Abbe's diagnosis of their variety is not especially detailed or precise but it is clear that the type specimen is a representative of the tall and robust, erect, moderately pubescent forms of *R. palustris* that are distributed at least in the north-eastern parts of U.S.A. and in E. Canada.

In 1940 Fernald identified var. *fernaldiana* with *Nasturtium palustre* var. *microcarpum* Regel. Regel (1861) erected this taxon on material from E. Siberia (Ussuri-region and Amur). He characterized his variety against the "genuine form" by its taller, strongly branched habit, thick stalk and small pods, which were not swollen and usually somewhat shorter than the horizontally patent pedicels.

Fernald (1940) erroneously[1] employed Regel's name but adopted later (Fernald 1948) the epithet *fernaldiana* for the amplified taxon. This has led to the view of var. *fernaldiana* (often named var. *microcarpa*) as distributed from E. Siberia to E. North America and rather sharply distinct from *R. palustris* of European type, which was considered as probably only introduced to North America (cf. also Hara 1952). This distinction was included in Gray's Manual (Fernald 1950) and many subsequent handbooks.

The identification of Regel's var. *N. palustre* var. *microcarpum* with the var. *fernaldiana* described from Maine does not seem to hold good. I have studied both the var. *microcarpum* specimen cited and photographed by Fernald (1940), which lacks notations by Regel, and a sheet from LE, which should be at least a syntype, since it was determined by Regel himself. Both were collected at the R. Amur by Maximovicz. The specimen studied by Fernald is rather poor, while the type is tall and branched and has very thin pods with a few small seeds (c. 0.4 mm). In contrast to ssp. *fernaldiana* it has many pairs of lateral leaf-segments, is practically glabrous and seems to be less robust. I have seen some similar specimens from Amur–Manchuria, but I will not express any opinion of the taxonomic significance of Regel's variety. Except for the pods it agrees well, however, with ssp. *palustris* and should at any rate not be included in ssp. *fernaldiana*.

In the Pacific area, from Alaska to California further taxa included in or close to *R. palustris* are met with, notably the tall, glabrous and extremely long-fruited *R. palustris* ssp. *occidentalis* (Watson in A. Gray) Abrams, and the Beringian species *R. barbareifolia* (DC.) Kitagawa, somewhat discussed in p. 85.

Comparison of the European and N.E. American populations

Fernald was doubtless right when he stated differences between North American and European *R. palustris*, but the specimens claimed (Fernald 1928) to reflect the differences and to be introductions constitute a mixed sample. I have seen five of these specimens, all in GH. Marie-Victorin & Romain-Rolland No. 27265, is not a *R. palustris* (cf. p. 66). The specimen Bissell, Bean, White & Linder No. 21326 has a sparse but distinct pubescence along the stalk, which is highly improbable for a plant of European origin. As to the remaining specimens seen (Macoun 11. VII. 1883, Nova Scotia, Perkins VII. 1878 and Robinson 8. VI. 1896, both Massachussetts) nothing contradicts that they have been introduced from across the Atlantic.

Since Fernald's statements were based on a heterogeneous material, and made without any detailed study of European *R. palustris*, it would be justifiable to discuss the question anew.

[1] Owing to the existence of *R. islandica* f. *microcarpa* (Beck) Thellung (1919), fide Fernald (1948), cf. p. 73.

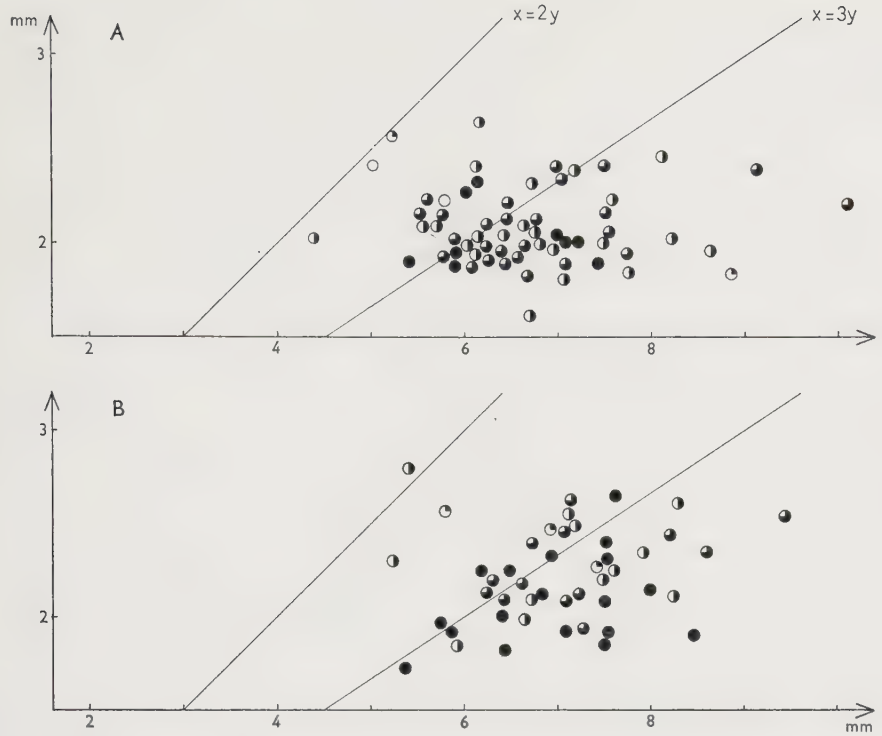

Fig. 9. *R. palustris*. Pictorialized scatter diagrams illustrating variation in *pod-length* (horizontal axis), *pod-width* (vertical axis), *leaf-shape* and *pubescence*. Leaf-shape is expressed as the mean value of pairs of lateral segments in all well developed cauline leaves in a specimen (cf. text). Open symbols = 0–2 pairs of segments; quarter-filled = 2.1–3, half-filled = 3.1–4, three quarter-filled = 4.1–5, and filled symbols = more than 5 pairs of lateral segments. Symbols with two lines = rich pubescence, one line = moderate pubescence, no line = sparse or no pubescence (cf. text). The diagrams A–H represent 8 geographical regions (see below). Each symbol represents one herbarium specimen (cf. App. 3) and the mean value of 10 measurements of each variate.

A = Central Europe and British Isles.
B = Denmark and Fennoscandia south of 60°N.

In order to obtain a basis for the discussion the diagrams in Fig. 9 were erected. The very wide and multifarious variation of *R. palustris* in North America and the not yet fully clarified taxonomic circumscription of it in the western parts, made it necessary to restrict a comparison with European material to a more limited area. Eastern Canada (North-West Territories, Manitoba and all states further eastwards) was chosen as being an important part of the area for Fernald's observations and since I have seen from there plenty of herbarium specimens, recently collected and in good condition (received particularly from DAO). The state of

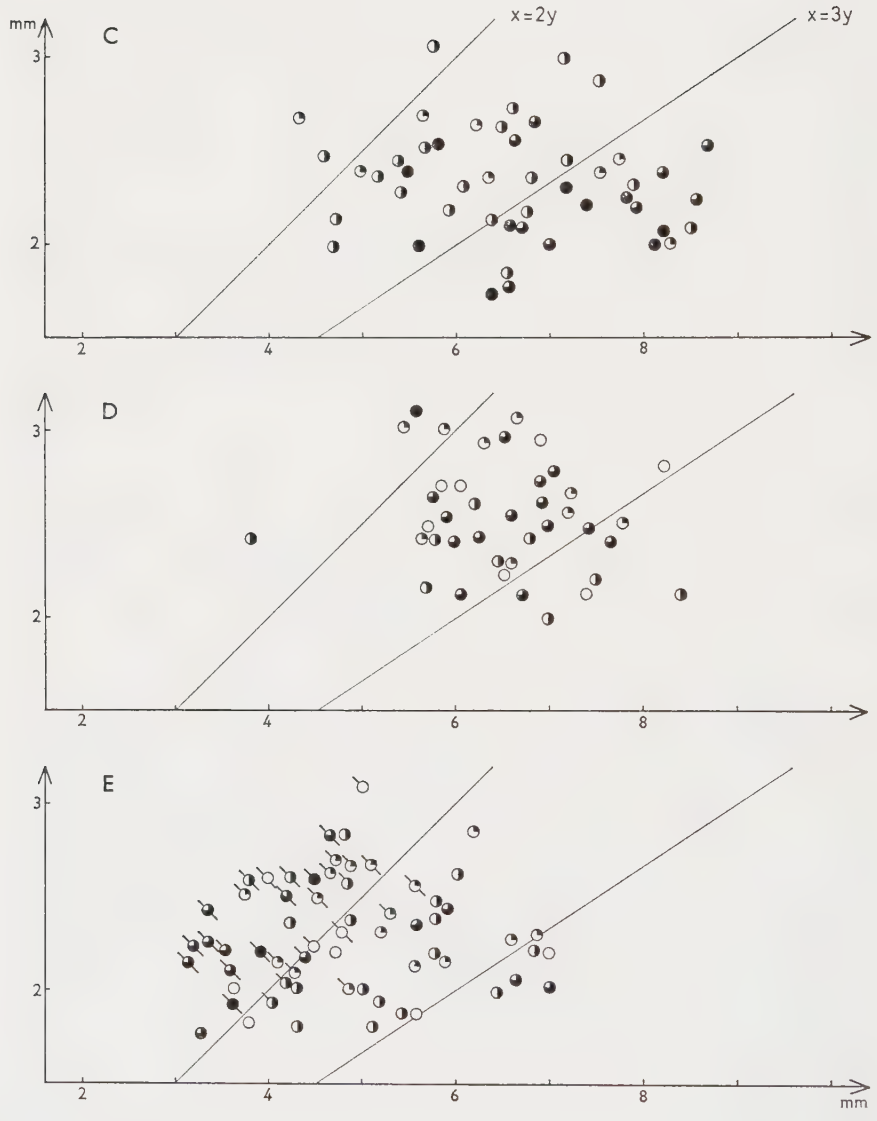

Fig. 9.

C – Fennoscandia between 60° and 65°N.
D = Fennoscandia north of 65°N.
E = Canada: Newfoundland, Nova Scotia, New Brunswick, Prince Edward Isl., Quebec, Labrador Terr., and U.S.A.: Maine.

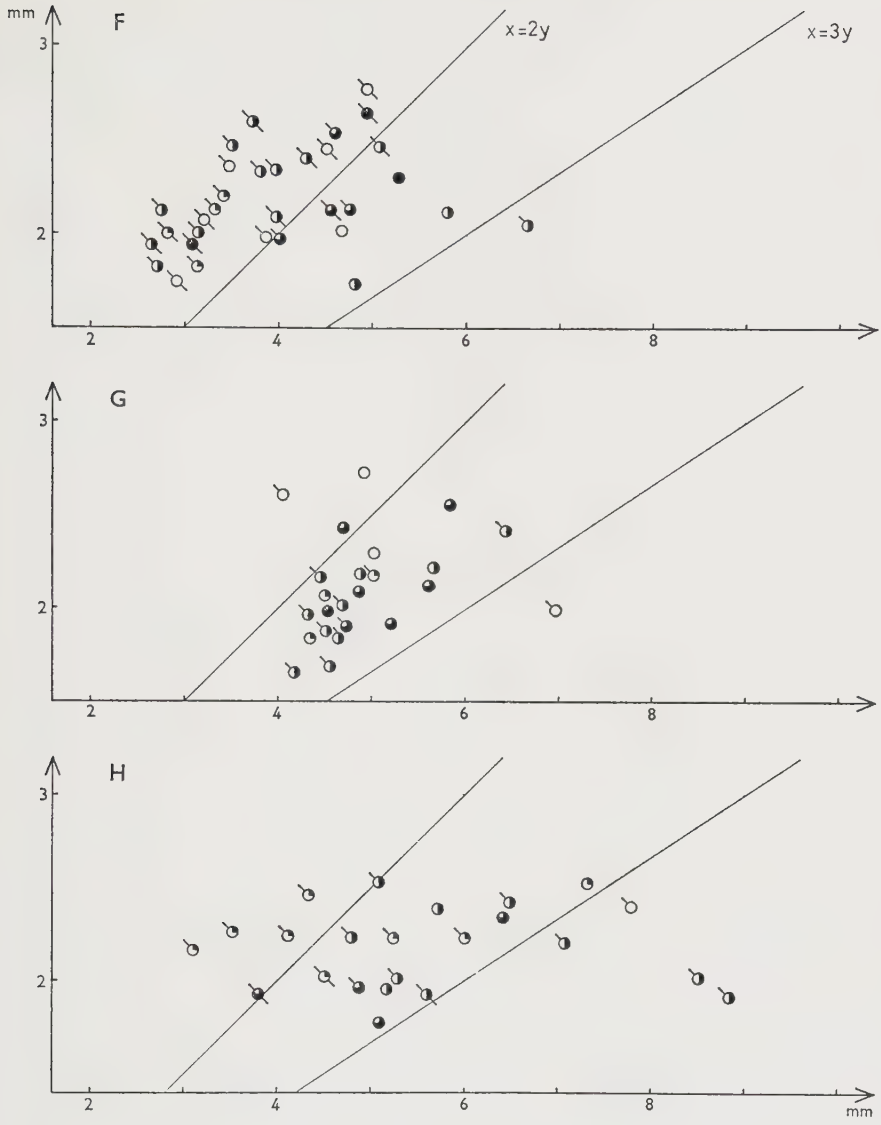

Fig. 9.

F = Canada: Ontario.
G = Canada: Manitoba.
H = Canada: North-West Territories.

Maine, U.S.A., was included, since *R. palustris* ssp. *fernaldiana* was described from there. The material was divided into four geographical groups, as it was thought to be of interest to see whether the variation pattern is the same throughout the area. The four regions are the North-West Territories, Manitoba, Ontario, and Quebec with the small East-Canadian states and Maine.

A comparison of all the diagrams in Fig. 9 shows clearly the great variability of N. American *R. palustris*. Most striking is the variation in pubescence, which strongly surpasses the very moderate amplitude in Europe (cf. p. 26). With respect to pubescence the material was grouped into three classes: strongly, moderately and weakly pubescent (cf. Fig. 9). The last-mentioned class was defined so as to cover the range of this character in the European material. Strong pubescence is present particularly in specimens showing other typical *hispida*-characters, but sometimes in other combinations. Moderate pubescence occurs in any combination with other characters. Many specimens are, however, as glabrous as European ones, but they may go beyond European variation in other features.

With respect to leaf-shape there is also a marked difference in the variation pattern, particularly when the American and S. Fennoscandian–Central European materials are compared. Leaves with numerous pairs of lateral segments together with narrow, more or less elliptic, terminal lobes, i.e. the characteristic European type (Fig. 5, K–N) exist but are rare in America. Besides the leaves typical of ssp. *hispida* (cf. p. 75), which are never seen in Europe, the American specimens have mostly few lateral segments and a long terminal lobe (Fig. 5 O). This is one of the main differences claimed by Fernald (1928) for *R. palustris* on the opposite sides of the Atlantic. But if also the material of Northern Fennoscandia is considered, the distinctions become obscure. Fig. 9 D shows a variation pattern for leaf-shape closer to the American material in Fig. 9, E–H (apart from ssp. *hispida*) than to the European material of Fig. 9, A–B. According to Fernald the American plants should also have thicker leaves, a character difficult to evaluate with certainty in herbarium material. As judged from the limited material in cultivation no conclusive differences exist on this point.

For pod-shape the diagrams clearly show a difference in variation pattern between American and European material, both with respect to relative and absolute size. In the American specimens the length/width ratio centers around 2, seldom reaching or surpassing 3, which is a normal value in most of the European regions. The American specimens have on the whole smaller pods than the European. But also on this point the North Fennoscandian material is rather intermediate between the American and the remaining European material. Among the features illustrated in Fig. 9, this shows the clearest difference between the American and European material, but there is considerable overlapping. The trends suggested by Butters & Abbe (1940) and accepted by Fernald (1940) can be seen, but are

not so clear as claimed there (cf. p. 75). The remaining features suggested to be more or less distinguishing between *R. palustris* on both sides of the Atlantic are either untenable or impossible to evaluate in dried material. Style-length is about equally variable on both sides of the Atlantic. The stigmata vary in N. American plants from distinctly capitate to non-capitate (especially in ssp. *hispida*) but are in Europe normally capitate. There seems to be a tendency for American plants to grow taller, and some specimens in cultivation (J 1137) rapidly exceeded Fennoscandian plants of the same age. But there are plants from Fennoscandia reaching a similar height (about 10 dm) even among those of typical European appearance in other respects. On the other hand some American plants may reach only moderate height in cultivation (J 1285). Plant height can consequently not be claimed as a distinguishing factor, though N. E. American *R. palustris* is probably on the average taller.

It should of course be critically examined as to whether the agreements between European and N. American *R. palustris* are quite simply the result of anthropochorous transport between the Continents. As mentioned above Fernald (1928) claimed European *R. palustris* to have been introduced to N. America, and above I gave an example of dispersal in the opposite direction (p. 73). This latter way must be negligible, however, otherwise there would not be such a homogeneity within the European material. Dispersal from Europe to America may well account for the existence in Fig. 9 E of a number of glabrous specimens of Central European leaf-type and a length/width ratio of the pods about 3. They are, in fact, from the St. Lawrence River, where introductions of plants through shipping is plausible (cf. p. 111). No specimens of that kind were found in the material from interior parts of Canada, where introductions from the other side of the Atlantic would be rarer, though it cannot be excluded that introduced specimens occur also there. Theoretically there could also exist segregational products from crossings between introduced and indigenous American plants, but there are no concrete indications of that.

There are, however, good reasons to believe that indigenous material from both sides of the Atlantic account for the most important agreements. This is especially supported by the fact that the similarities are the greatest with the material from northernmost Europe, from where anthropochorous transport of *R. palustris* across the Atlantic must be of minor importance. The glabrous American specimens showing the greatest agreements do not either give the impression, according to the labels, of being anthropochores in any higher degree than the rest of *R. palustris*. All forms of the species seem in N. E. America to be found at the margins of lakes and rivers, as well as apophytically or as anthropochores at roads, in fields etc.

The material from the North-West Territories (Fig. 9 H) shows a variation pattern somewhat divergent from the other groups of American material. There is, apart from pubescence, a slightly greater coincidence with Northern-Central Fenno-

scandian material. Specimens showing such coincidences are still more frequent in Yukon-Alaska, and it is obviously a connexion in this direction that is manifest here. Whether there is a further distributional connexion between Alaskan and North Fennoscandian material via Siberia is quite unknown. A comparative study of *R. palustris* from these regions must be performed before a full taxonomic treatment of the Holarctic *R. palustris* is possible.

The most essential conclusions from the account above will be: *R. palustris* is in N. E. America much more variable than in Europe but the variation patterns are partly overlapping. A good number of specimens are easy to classify as to their original Continent. Difficulties on this point arise particularly for plants from northernmost Fennoscandia. Within the Canadian *R. palustris* population such specimens constitute a fraction of the material over the whole area surveyed, but seem to be more frequent in the N. W. Territories. It should be emphasized, too, that all present evidence points to an agreement in chromosome number for all the material concerned here (cf. p. 68).

Taxonomic conclusions

R. palustris shows on both sides of the Atlantic a wide range of variation, where no clear discontinuities are manifest. The variation is partly only local, implying aberrancies in single features, and then taxonomically of little significance. But there is also the continuous variation towards extremes of well-defined appearances and geographical ranges. Such a situation in Fennoscandia has already been discussed and found not to warrant taxonomic separation (cf. p. 72). In North America much more marked extremes are found. Also there, however, a great amount of the material will be difficult to place in any infraspecific scheme. It might therefore be suggested that no infraspecific separation at all should be undertaken. But this would be to hide important differences that for both practical and theoretical reasons should be taxonomically recognized.

Within the region concerned ssp. *hispida* is at first hand worth recognizing as a taxon. It is variable and shows numerous transitions to other taxa but is held together by a number of conspicuous characters (cf. p. 74 and Ch. 8) and is confined to a limited part of the distributional range of *R. palustris*, although it is there not the only taxon of that species. Subspecific rank seems most natural for a taxon of this kind, while status as a separate species is untenable.

It would be clear from the preceding discussion that ssp. *fernaldiana* is more difficult to characterize and circumscribe than ssp. *hispida*, since it is not an extreme in such conspicuous features as this one. It would be distinguished through its tall, erect and robust shoots in combination with faintly pinnate leaves (cf. Ch. 8), while considerable variation must be allowed in pod-shape and pubescence. The pods are on the whole smaller than those of ssp. *palustris*. With some hesitation I accept, however, ssp. *fernaldiana* as a taxon parallel to ssp. *hispida*, which is

in accordance with current use. An alteration of its status should be based upon a more intense study of *R. palustris* in the whole of N. America.

The two subspecies should preferably be circumscribed in a narrow way, so that they represent only just the extremes and show comparatively little internal variation, at least in decisive characters. Only if they are clearly defined, can matters of distribution and dispersal be assessed for them and employed in discussions.

After the extremes have been cut off a very variable and widely distributed taxon inevitably remains. Since it includes the type of the species (cf. Ch. 7) it will automatically obtain the name ssp. *palustris*. It cannot be denied that ssp. *palustris* with respect to variation and distribution would be fairly incongruent with the other subspecies. It might be possible to make a more delimited circumscription of ssp. *palustris* allowing it only to comprise the characteristic plant of the cultivated parts of Europe. This would, however, make the taxonomic status of all that is between this plant and other extremes very problematic. Though a limited material was studied there is good evidence that *R. palustris* of chiefly European appearance is distributed spontaneously throughout Siberia and in other parts of Asia (e.g. J 1079, 1539) but perhaps together with other forms. Moreover *R. palustris* specimens which with certainty can be claimed to be aliens in a region, are mostly in morphological agreement with European plants, while e.g. typical American forms have only occasionally been noticed in such connexions (cf. p. 73). This is of course up to expectation if communicational history is considered. This means that weedy *R. palustris* of European-Asiatic origin has had much time to be intermixed over vast regions with spontaneous populations, which may have merged into a population with a continuous variation pattern (cf. p. 72). For this reason it seems most natural to let ssp. *palustris* cover all this wide gradual variation, as there can be no satisfying taxonomic subdivision made within the mixture of spontaneous and introduced populations. In regions where a more drastic morphological variation with correlation between some features is apparent and where weedy introductions only recently have begun to play a part, the recognition of further infraspecific taxa would be possible and also desirable.

One example of that is ssp. *occidentalis* (cf. Ch. 8), which I have not studied critically but all the same dare regard as a taxon of subspecific rank. *R. palustris* from N. W. Canada and Alaska is often treated as var. *williamsii* (Hultén) Britton, described from Yukon Terr. I will not express any opinion of that taxon, but my own cultivated Alaska specimens fall clearly within ssp. *palustris* in the wide sense taken here.

The wide circumscription of ssp. *palustris* implies that not only all European, but also a good number of reasonably indigenous N. American plants will be attributed to it. This is in accordance with my view that in *R. palustris* clearer

taxonomic limits can be drawn on the N. American Continent than between N. America and Europe.

Survey of the *Rorippa islandica* group

From the morphological and biological evidence given above it seems clear that the species *R. islandica* and *R. palustris* together with a number of exclusively N. American species, only a few of which will be mentioned here, constitute a group of very closely related taxa, which from all present knowledge appears to be well separated from the rest of the section *Rorippa*. The most important criteria of this group are the limited life-length of the individuals and the marked autogamy, which has probably led to the small flowers present throughout this group. There are obviously good reasons to expect this group to have evolved for considerable time within its own boundaries, devoid of influence from the rest of the section — apart from hybrids which would be evolutionarily insignificant (cf. p. 160).

It seems natural to regard the *R. islandica* group as derived from perennial and large-flowered species of the section. The taxa of the latter type are more disparate, and there are groups among those which are rather isolated (e.g. the *R. pyrenaica* group, cf. Ch. 1). Also the sections and genera of closest affinity are, as far as is known, mostly perennial and large-flowered. This would therefore be the primary stage of the section *Rorippa*, from which a small-flowered, autogamous group of species has evolved. Very good reasons for annual species with reduced size in diverse organs to be advanced in comparison with perennial ones have been put forward in *Crepis* (Babcock 1947).

The evolutionary history within the group can be traced only to a minor extent. It rests upon the fact that we can state polyploidization, but only to tetraploidy, and that diploid cytotypes have proved to occur in various taxa of restricted distribution, while tetraploids are found within the widespread *R. palustris*.

From the following taxa and regions diploid individuals ($2n = 16$) were found (see also App. 1): *R. islandica*, for which diploidy has been proved in the Atlantic region only, *R. barbareifolia* from Central Alaska (J 574), *R. curvisiliqua* from California (J 1281), Oregon (Rollins 1966) and British Columbia (Mulligan 1964), *R. curvipes* (cf. p. 65) from Colorado (J 1289, Rollins 1966), Wyoming (J 1286), Saskatchewan (J 1128, 1476) and British Columbia (Queen Charlotte Island, J 1288, see below) and finally *R. sessiliflora* (J 1479) from Arkansas. It is probably not only because of the limited material that except for *R. islandica* diploid counts only occur from western North America, since it is clear that the richness of taxa of this group is there the greatest to be found anywhere.

The species *R. barbareifolia* (DC.) Kitagawa may morphologically be summarized as an utterly extreme *R. palustris* ssp. *hispida* showing a very rich

pubescence (cf. p. 26), tall and erect growth, markedly acutely angled leaf-segments and very large (c. 9 × 5 mm) spheroid pods. In contrast to the other diploids known its flowers are of about the size found in *R. palustris* with petals about 2.5 mm. This species has a Beringian distribution (Siberia by the rivers Yenisey, Lena and Amur, Alaska and Yukon). It lies close at hand to assume this species to have taken part in the origin of *R. palustris* ssp. *hispida*, in which tetraploids have been found and which is partly sympatric with *R. barbareifolia*. Some authors, e.g. Hultén (1945), have regarded *R. barbareifolia* as a subspecies under *R. hispida* (cf. p. 74). This taxonomic question is outside the present study, but there seems to be a much more marked discontinuity between *R. barbareifolia* and *R. palustris* ssp. *hispida*, than between the latter and ssp. *palustris*, quite apart from the difference in chromosome number. *R. barbareifolia* is also sometimes considered as an extreme of the tall, glabrous Pacific *R. palustris* var. *occidentalis* (cf. p. 159, Fernald 1940).

Since western N. America constitutes the chief center of diversity of the *Rorippa islandica* group, and since we have there a number of diploids more or less close to *R. palustris* it seems reasonable to suspect processes of allopolyploidy and perhaps also autopolyploidy, leading to the origin of tetraploids approaching *R. palustris* of today to have taken place there. Although sharp distinctions are reported e.g. between *R. curvipes* and *R. palustris*, there is a general agreement between the species, much reminding of the situation *R. islandica v. R. palustris* in Europe. *R. islandica* might have acted in a similar way in Eurasia. The great resemblance between most European *R. palustris* and the diploid *R. islandica* on the one hand, and between the N. American *R. palustris* ssp. *hispida* and the Beringian species *R. barbareifolia*, at least partly diploid, on the other, can hardly be only accidental. The variation patterns of these diploids have obviously been brought together on the tetraploid level, but there should be genetic material also from elsewhere, e.g. from forms approaching *R. curvipes*, to account for the variation observable in *R. palustris* today. So it is possible that the forms united under the name of ssp. *fernaldiana* originated from crossings between plants approaching ssp. *hispida* and ssp. *palustris*, but special features make the participation of some more taxon probable.

The ultimately resulting, vastly distributed, variable tetraploid — *R. palustris* — was successful as a weed in a much higher degree than *R. islandica*, at least, and probably the other diploid taxa, too. This circumstance has certainly contributed much to the variation pattern seen today, but it is impossible to know how and to what degree in various regions. Thus we have probably within this group the evolutionary model, where a stock of more or less isolated diploids has given rise to a number of tetraploids highly successful as colonizers over new areas, which has led to that they met and partly merged.

The group is much too little known not to hide other patterns of evolution,

particularly in N. America, which may change the view of the one outlined. This is only an attempt to an interpretation of the facts known at present and may serve as a base for further discussion.

B. *Rorippa sylvestris*

Variation and Taxonomy

R. sylvestris is apparently indigenous only in certain parts of Europe and in Western Asia but introduced to many places outside this area (cf. p. 95 f. and Ch. 8). The considerable morphological variation within the species has been frequently observed and led to the description of infraspecific taxa, none of which, however, is based on N. W. European material. Some more important of those taxa are mentioned on p. 96. Much of the variation described, particularly in Central Europe, is obviously due to hybridization, above all with *R. amphibia* and *R. austriaca* (cf. Ch. 6 D). The limits to what should be classified as hybrids with these species is sometimes diffuse also in N.W. Europe. It is of course a question of more practical than theoretical significance. As *R. sylvestris* will here be treated all material that does not show characters clearly indicating influence from other species. Plants showing such characters are classified as hybrids and treated in Ch. 6 D.

Cytotypes

In Scandinavia, where about 50 spontaneous samples were investigated, the two primary cytotypes ($2n = 32, 48$) are about equally scattered over the range of the species. Ecological differences between the cytotypes (cf. p. 93) contribute to differences in local distribution, e.g. in the Mälar region, and to the circumstance that examined outposts in the north are all hexaploid (cf. Fig. 13). Also a determination reported from Iceland (Löve & Löve 1956) was hexaploid. The pentaploid cytotype, known from only two stations (J 357, 865) is probably derived from the other two (cf. p. 41).

In the extra-Nordic material the tetraploids dominate, and occur in France (J 1074, 1135, 1587), Portugal (J 962, 1127, 1463), Yugoslavia (J 1116, 1384, K. Larsen 1956, publ. as *R. islandica*), Hungary (J 958, 1129, 1465) and Rumania (J 1577). From Britain two tetraploid hybrids very close to *R. sylvestris* occur (J 1171, 1172) that certainly derive from back-crosses to tetraploid *R. sylvestris*. Hexaploids are known only from Britain (J 1165, Howard 1946), the Netherlands (J 1567) and France (J 253).

The studies of morphological variation in *R. sylvestris* aim partly at evaluating the degree of correlation between chromosome numbers and other characters

Table IV. Pollen fertility in spontaneous *R. sylvestris.*

Cytotype	Number of samples	Percentage stainable pollen grains											
		0	1	10	20	30	40	50	60	70	80	90	100
Tetraploids	27	2	2	5	1	3	4	3	1	1	4	1	
Pentaploids	2	1	—	—	—	—	—	1	—	—	—	—	
Hexaploids	35	17	2	2	—	6	3	4	1	—	—	—	

In the group with < 1 % of fertile grains are 1 tetraploid and 14 hexaploids with nonaperturate pollen.

and partly at creating a basis for putting the same characters in relation to growth-place and distributional history in Scandinavia.

Relations between pollen shape and cytotypes

As mentioned in Ch. 3 the normal pollen with reticulate walls is much more variable in *R. sylvestris* than in the other species treated here, both within a specimen or a clone and between different clones. The variation makes comparative size measurements of *R. sylvestris* pollen rather useless. The ratios between tricolpate and tetra- to pancolpate grains are, however, to some extent correlated to the cytotype. In all tetraploids examined the tricolpate grains dominate (i.e. constitute more than 2/3 of good grains), and mostly the tetracolpate grains are very few. The hexaploids are more variable, but tricolpate grains dominated only in 3 of the 14 samples with colpate grains investigated.

Most *R. sylvestris* clones have reduced pollen fertility but on the average a greater proportion of sterile pollen is found in hexaploid than in tetraploid clones, and only among the latter there are clones with pollen of good quality (cf. Table IV). Such a tendency is up to expectation in plants derived by a process approaching autopolyploidy, which would be valid for the hexaploids (cf. p. 97). In induced autopolyploids a higher ratio of aborted pollen grains was noted in the higher polyploids by Maurizio (1956). In spontaneous and experimentally produced pentaploids, as well as in the aneuploids usually less than 50 % of the grains are stained, but most of them have a certain amount of morphologically well developed grains. Many grains, however, although stainable have a thin or in some other way aberrant exine.

Erdtman (1958) recorded nonaperturate grains in a fourth of his material that was chiefly Scandinavian. In a greater material this pollen-type was found to be much rarer, occurring only in about 10 % of the Nordic herbarium material examined. Nonaperturate grains were found in both tetraploid and hexaploid spontaneous clones. The single tetraploid seen in Fig. 10 is the clone J 186,

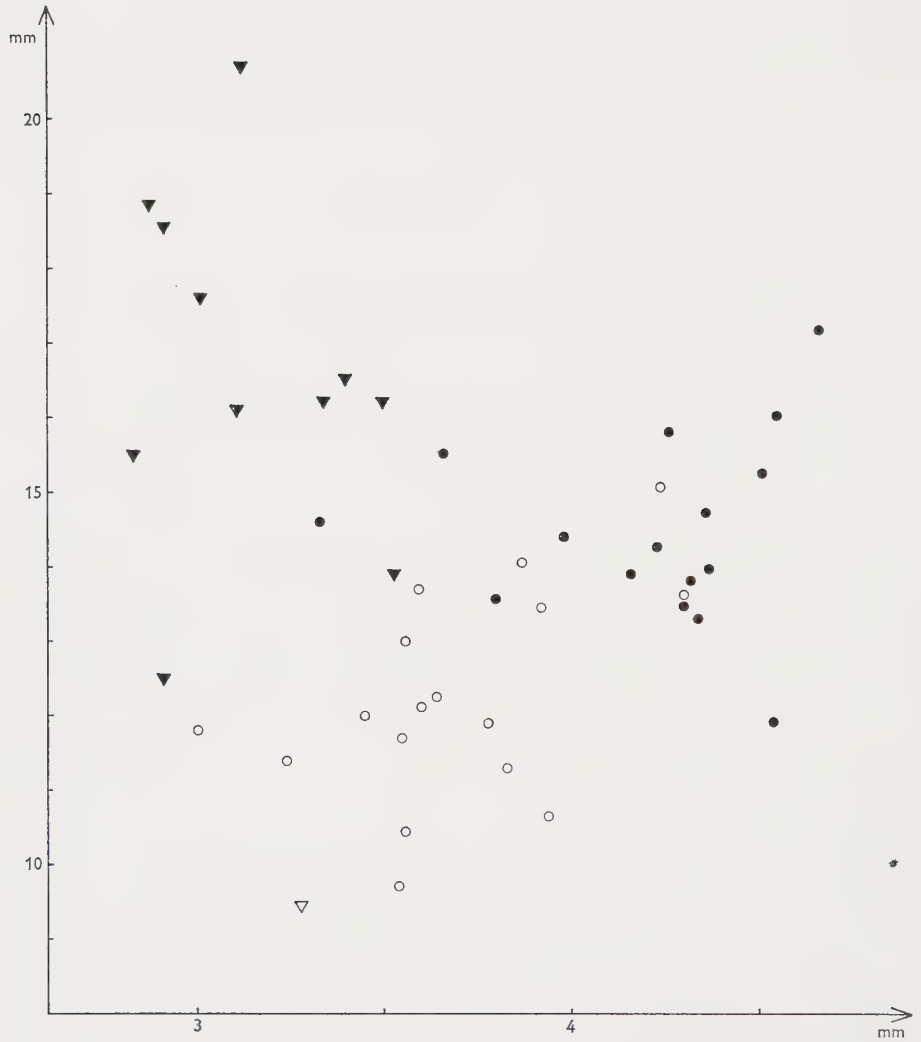

Fig. 10. *R. sylvestris*. Scatter diagram illustrating combined variation of *petal length* (horizontal axis), *pod-length* (vertical axis), *chromosome number* and *pollen type* in Nordic material. ○ = tetraploids with colpate pollen; ● = hexaploids with colpate pollen; ▽ = tetraploid with nonaperturate pollen; ▼ = hexaploids with nonaperturate pollen. Each symbol represents one cultivated clone and the mean value of 10 measurements of each variate.

further discussed in p. 91, and most pollen is there actually amorphous. In a number of hexaploid rhizoclones (J 143, 171, 859, 877, 886, 912, 1082, 1083, 1113) the nonaperturate grains are rather regular in shape and there are few amorphous pollen fragments seen. These clones are further discussed below, since they display some particular features with respect to morphology and ecol-

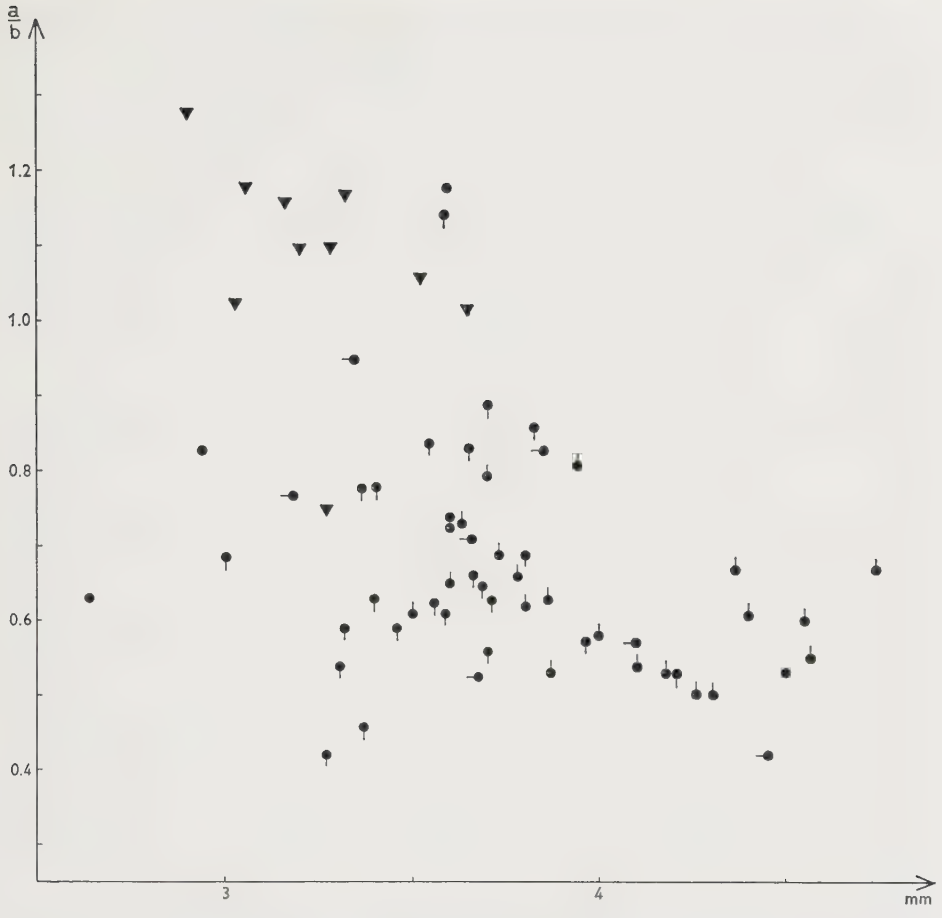

Fig. 11. *R. sylvestris*. Pictorialized scatter diagram illustrating combined vatiation of *petal length* (horizontal axis), ratio of *length of unfertilized gynecia* (a) to *pedicel length* (b) (vertical axis), and *pollen type* in Nordic material. Triangles = nonaperturate pollen; dots without lines = amorphous pollen; dots with line downwards = colpate pollen, $> \frac{2}{3}$ tricolpate; dots with horizontal line = colpate pollen, $\frac{1}{3}$–$\frac{2}{3}$ tricolpate; dots with line upwards = colpate pollen, $< \frac{2}{3}$ tricolpate. Each symbol represents one herbarium collection (cf. App. 4), none of which is included in Fig. 10, and the mean value of 10 measurements of each variate.

ogy. In other hexaploids the nonaperturate grains are of a less regular shape (e.g. J 963, 1103). It should be stressed that nonaperturate pollen was never seen in any clear *R. sylvestris* hybrid.

Variation in reproductive characters

Few previous observations exist on gross morphological variation in Nordic *Rorippa sylvestris*. Nearly all discussion on the point treats hybrids or what was

thought to be hybrids. In many cases specimens of *R. sylvestris* were erroneously considered hybrids, most notably with *R. palustris*. The causes of this view were apparently mostly the observations of the unfertilized gynecia normally present in *R. sylvestris* under natural conditions (cf. Ch. 3), and of the small petals, which exist in many clones and were seen as an influence of *R. palustris* (cf. below).

Two pictorialized scatter diagrams (Figs. 10, 11) give a survey of the morphological variation in Nordic *R. sylvestris*. In both of them the variation in petal length is included as a variate. It is seen that the normal variation of petal length reaches from below 3 to nearly 5 mm, but there are also single specimens with abnormally reduced petals (Albakgård, 1958 A. Hansen, C; 1859 Lange, C). The amplitude of the variation within a rhizoclone is usually less than 0.5 mm in comparable flowers (cf. Ch. 3), but there are examples of a greater variation. In the clone J 185 flowers of extremely varying size (petals 3.3–4.7 mm) are present contemporarily, and hence this clone was excluded from Fig. 10. This great variation seems to be connected with the highly varying pollen quality of J 185. Sepals and stamens vary very closely in relation to the petal length, which is here thought to be the most convenient expression for flower size on the whole.

Also the ripe pods, included as the other variate in Fig. 10, show considerable variation in length, c. 10 – c. 20 mm. This character is measurable only in plants kept in cultivation (cf. p. 33). The two spontaneous pentaploids are excluded since frequent abortion prevent their pods ever to reach what can be estimated as the full length. In Fig. 11, based entirely on herbarium material, the ratio between length of unfertilized gynecia and pedicel length was used instead. Also this character ratio varies continuously over a wide range, c. 0.4–c. 1.3. In both diagrams the pollen type of each specimen is included. In Fig. 10 the cytotype is visualized as well.

The variation in all these features is by no means at random, but obvious correlation can be discovered. Among the plants with colpate pollen there is, as seen from Fig. 10, a pronounced tendency for the hexaploids to carry both longer petals and longer ripe pods than the tetraploids, but there is no sharp limit between the groups. Single specimens fall quite outside the swarm formed by the bulk of those with colpate pollen. But some tetraploids from L. Mälaren that probably show signs of introgression from *Rorippa amphibia* (J 892, 929, cf. p. 122) contribute to make a limit along the characters discussed still more diffuse. In some tetraploids the petals are not only short but also very narrow (< 1.7 mm). They are discussed in p. 95.

The herbarium material represented in Fig. 11 gives a similar picture with respect to petal length variation, since in specimens with colpate pollen this is correlated with the ratio of tricolpate grains. This ratio would namely as previously discussed (p. 87) give a certain idea of the cytotype, perhaps in so far that a majority of specimens with a predominance for tetra-to pancolpate pollen can be

assumed to be hexaploids, while most of those with preponderate tricolpate grains would be tetraploids. For the character ratio employed as the other variate in Fig. 11 there is no correlated variation to be traced within the material with colpate pollen.

Specimens with the nonaperturate, unfunctionable pollen are seemingly aberrant in other reproductive characters, too. They have all very short petals (as well as stamens and sepals), though not necessarily shorter than those in plants with normal pollen. From Fig. 10 it is seen that the only nonaperturate tetraploid (J 186) found agrees on the whole with other tetraploids both in petal length and pod length. The hexaploids with nonaperturate pollen constitute in Fig. 10, however, a group on the whole well separated from the hexaploids with colpate pollen. The short petals which are mainly responsible for this discontinuity might, as mentioned, be directly connected with the male sterility. But oddly enough the same plants carry ripe pods of lengths often surpassing those found in any other clones, as they may reach and even exceed 20 mm. These pods are as narrow as those of hexaploid *R. sylvestris* in general (c. 1.2 mm) but often curved like a sickle. Turning to Fig. 11 it will be seen that the specimens with nonaperturate pollen are on the whole grouped together, as distinguished by long unfertilized gynecia in relation to the pedicels. There the unfertilized gynecia almost equal or surpass the pedicel length, while they are comparatively shorter in plants with colpate pollen. In the latter group the unfertilized gynecia are sometimes very short (c. 3 mm), but in general a long pedicel causes the distinction from specimens with nonaperturate pollen, where an inhibition of the normal prolongation of the pedicel after anthesis has seemingly occurred. There the pedicels are horizontal and not slightly ascending as is normal in *R. sylvestris*. Disturbances of normal prolongation seem to affect also the whole fruiting racemes, whose axes run in a zigzag-like (flexuous) manner between the compactly sitting pedicels. This last-mentioned feature is pronounced, however, only in some of the specimens with nonaperturate pollen (cf. p. 94).

Variation in vegetative characters

There are a number of vegetative characters which show a more or less pronounced correlation with the reproductive ones represented in Figs. 10, 11. Most conspicuous is the variation of the shape of the lateral leaf-segments, which as a rule are almost free from each other at the base. Fig. 12 shows a number of cauline leaves from plants in cultivation. At one extreme (Fig. 12 E) the lateral segments are long and narrow with a very sparse denticulation. The laminae of such leaves become proportionately broad. More often a rather prominent denticulation is present (Fig. 12 D, I). This type of leaves is by far the most widespread in the cultivated material, both in tetra- and hexaploids, and apparently in the Nordic herbarium material, too.

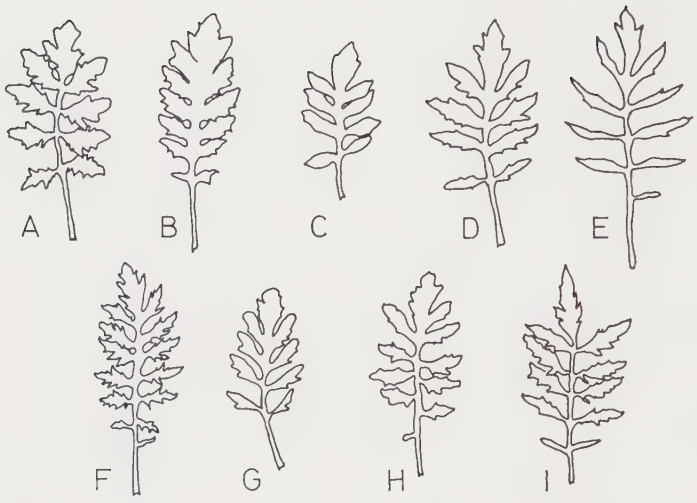

Fig. 12. Cauline leaves of *R. sylvestris*. A–E: hexaploids (A: J 877. B: J 890. C: J 581. D: J 869. E: J 401). F–I: tetraploids (F: J 916. G: J 361. H: J 929. I: J 441). All leaves from specimens in cultivation. ½ ×.

Rather striking is a leaf-type with segments mostly somewhat rounded at the apex (Fig. 12 G, Plate XI). This type is found particularly in a group of tetraploids, and is on the whole restricted to plants with narrow petals. These leaves are on the average smaller than the other types, a feature connected with a less vigorous, rather slender appearance of the whole shoots. Very rarely leaves with such rounded segments were observed in hexaploids (J 581, Fig. 12 C).

Another extreme type of leaves is represented by Fig. 12, A, F. There the segments are short and broad with a coarse denticulation, sometimes approaching a bipinnatifid arrangement. The lamina is comparatively narrow. This leaf-shape occurs in some tetraploid clones (J 916, 439) but is particularly characteristic of hexaploids with nonaperturate pollen, among which a remarkably constant leaf-shape is found throughout most of the group (Plate IX). The leaves of those hexaploids mostly have a more bluish-green tinge than is usual in the rest of *R. sylvestris*, a character visible in living plants only.

From this account it is seen that there is some correlation between the variation of leaf-shape and other features, but this is valid only for certain groups within the material. For the rest the variation seems to give combinations more at random. Recent introgression may be of importance for variation on this point, too (cf. p. 123).

The vigour and height of the shoots vary considerably. The shoots of most clones studied are ascending, at least under conditions present in cultivation. An exception is the clone J 185, where the shoots are short, rather prostrate and

richly branched, thus forming almost a mat. Another aberrant type of shoots occurs in hexaploids with nonaperturate pollen. Here the shoots are strikingly erect, which together with the flexuous inflorescence (cf. p. 91) gives to those plants a recognizable appearance (cf. Plate IX).

The hexaploids are on the average more vigorous than the tetraploids. Extremely vigorous clones are e.g. the hexaploid J 1068, and also the pentaploid J 357, where single shoots may reach about 90 cm. The vigour of shoots is on the whole correlated with the vigour of the subterranean root runners, which are of great importance for dispersal (cf. Ch. 4). The greater success for the hexaploids as weeds (cf. p. 102) may be due to differences between the cytotypes in these respects.

Much other variation was observed in diverse features within the material. Part of this variation, comprising e.g. auricles, width of pods, style-length, is of particular importance for evaluating hybridization, and is therefore treated only in Ch. 6D.

Conclusions about intraspecific variation

From the above account it is clear that at least in Nordic material it is possible with some probability to state the cytotype of a specimen from its morphology, as long as only tetraploids and hexaploids are involved. There is apparently along with the morphological variation also a variation in ecological preferences within the species. Tetraploids only were found under fairly natural conditions, i.e. on shores. Other tetraploid clones, however, grow completely as weeds also in rather dry places, e.g. in gardens, waste-places, at roads, where they are certainly not apophytes only. The hexaploids, on the other hand, were mostly found as weeds. In cases where hexaploids were found on shores usually artificial banks were colonized (J 581, 602), or the plants could be suspected to be recent neophytes (J 1235, 1307). Outside Scandinavia hexaploids were found at the banks of the river Thames, though in far from natural environment.

Erdtman (1963*b*) suggested that plants with tricolpate pollen should emanate from a "statocratic" environment and those with nonaperturate or otherwise irregular pollen from an "apocratic" (definitions in Erdtman op. cit.). If "statocratic" would only mean a fairly natural environment this is in accordance with the ecological tendencies mentioned in so far as the first group is mainly tetraploid, the second to a great extent hexaploid. For many clones not even such a suggestion is valid, however, and moreover *R. sylvestris* is actually always an "apocrat" since it nowhere was found in stable environment.

The data presented make clear that in Nordic *R. sylvestris* there is a considerable variation and even striking aberrancies in a number of features. Parts of the heterogeneous material can be assorted into some fairly homogeneous groups with more than quite local distribution. Such a group would either consist of a single clone, which has gained considerable distribution, or of a group of closely

related clones. Here only the characteristics of three important groups within Nordic *R. sylvestris* will be summarized.

Hexaploids with nonaperturate pollen. The most apparent group is doubtless composed of the hexaploids with nonaperturate pollen, associated with small flowers, nearly bipinnatifid leaves, flexuous inflorescences etc. (cf. above, Figs. 10, 11, Plate IX). It must be stressed that all these features may occur independently of each other in clones with normal pollen. There are a number of rhizoclones (J 143, 171, 859, 877, 886, 1082, 1083 and 1113 in the cultivated material) which show all the characteristics mentioned and display only small differences between each other. Herbarium sheets of this type were found from some tenths of localities scattered over Denmark and S. Fennoscandia. A great majority of the finds emanate from garden soil (in nurseries, parks, cemeteries etc.), with which these plants are apparently dispersed. Many of the samples mentioned above may belong to one clone, but a few show morphological (J 143) or cytological (J 1082, cf. p. 19) discrepancies that indicate that they are genetically separate from the rest.

Some other collections of hexaploids with nonaperturate pollen show few or none of the gross-morphological characteristics mentioned and must certainly represent other clones. An illustrating example is the plant J 912 from Visby (Gotland), which is distinguished from other hexaploids with the actual pollen-type particularly through the lack of the flexuous axis of the fruiting raceme. This clone can be traced back in herbarium material from Visby to 1863, and was collected many times during the last hundred years (cf. also p. 101). Among the cultivated material the rhizoclones J 963, 1103 and 1234 represent other hexaploid clones with nonaperturate pollen.

From outside Scandinavia very few collections with nonaperturate pollen were seen. No complete investigation was made on this point, but pollen samples were examined from a number of specimens in the herbaria listed in Ch. 1. One collection from Portugal (Fernandes, Matos & Matos No. 5670, BM) has rather imperfect nonaperturate pollen, and is also morphologically outstanding among *R. sylvestris* with its unusually stiff and parallel fruiting branches and scattered hairs even high up on the plant. The leaves are similar to those of Nordic plants of the same pollen type, but the cytotype is of course unknown. This collection was taken at the margin of R. Douro, and is obviously also ecologically different from the Nordic clones.

Hexaploids with colpate pollen. A second fairly homogeneous group consists of the hexaploids with long petals, leaves with narrow segments (Fig. 12 E, Plate X), and with often vigorous habit (J 401, 531, 960, 1068, 1243, 1254). There are probably a lot of clones of approximately this model. These clones are also weeds, to a great extent in gardens, but also at roadsides, harbours and waste-places. Being much

less homogeneous than the former group it is also much more diffusely separated from the rest of the species. It seems plausible that these morphologically similar clones really have a history of origin in common, but it has not been possible with sufficient security to relate the group to any extra-Nordic *R. sylvestris* although many sheets of apparently similar type exist from Central and Western Europe. Some tetraploid clones (e.g. J 441, 870) are morphologically close to this group but not so vigorous.

Tetraploid shore forms. A third group rather outstanding as to morphology consists of the tetraploids with a slender habit, rounded leaf-segments, narrow and rather short petals, and ripe pods not exceeding 15 mm (cf. Plate XI). Also here many clones are present within the group. They are primarily found at sandy-gravelly lake shores etc., but are markedly hemerophilous. All the same they have never been seen as real weeds. They are chiefly found in the Mälar-region (J 361, 891, 892, 918, 1388), where they show a broad variation evidently due to introgression (cf. Ch. 6 D). Clones of about the same appearance were seen also from other water systems (e.g. J 620), and probably some South Scandinavian herbarium specimens seen should be taken to this group. Also for these clones there are more or less striking accordances with extra-Nordic specimens, especially from S. E. Europe (e.g. J 1465). This does not, however, permit any conclusions on connexions.

Each of the three groups of clones discussed represents an extreme of the variation range of a number of features, a matter which naturally strongly contributes to the ability to recognize them in the material. As a rule we have a continuous variation in all features discussed here, and most of the clones studied cannot be placed within any of those groups. As to the taxonomic treatment of the intraspecific variation arguments could be raised to discern e.g. the easily recognizable hexaploid with nonaperturate pollen as a taxon of low rank. Since it cannot be circumscribed with full accuracy and since taxonomic rank would equally justify the recognition of other recognizable clones or groups of biotypes, I prefer not to discern any infraspecific taxa.

Affinities to extra-Nordic taxa

Also outside Scandinavia *R. sylvestris* is obviously both cytologically (cf. p. 86) and morphologically variable in no less degree. According to several authors (e.g. Hegi 1958–63, Lawalrée 1955–57) the plant is frequent in many Central European lowland regions, and would be rich in biotypes quite apart from those derived from hybridization with other species (cf. p. 38). Primarily it was there probably an alluvial plant but it is very common as a weed, and to distinguish between indigenous and neophytic occurrences will there be still more difficult than in Scandinavia. There are few regions known where *R. sylvestris* grows in an environment,

where it with certainty can be regarded as indigenous. In Russia it is an alluvial plant even far to the north (Onega-valley acc. to Cajander 1905), but might well be a neophyte.

A population in arid, saline ground in Hungary is referred to as *R. sylvestris* ssp. *kerneri* (Menyh.) Soó & Jávorka (also as species *R. kerneri* Menyh.), and is probably the result of an ecological specialization within the species (cf. Borsos 1951, 1967). In Turkey most finds are from marshes and shores, very few from cultivated ground (Davis 1965), and the specimens seen by me fall well within the variation range of *R. sylvestris*. In S. E. Europe *R. sylvestris* seems to display partly a variation pattern not seen elsewhere, which has led to the description of infraspecific taxa from this area (cf. Hayek 1924–27). In western Turkey and in the Balkans there are also some taxa morphologically very close to *R. sylvestris* that are doubtless indigenous in the region. One is *Rorippa prolifera* (Heuff.) Neilr., which both according to Davis (1965), who gave to it subspecific rank, and my own preliminary observations is not sharply distinguished from *R. sylvestris* of those regions. Also the species *Rorippa aurea* (Boiss.) Huber-Morath, known only from very few Turkish collections, seems to be close to *R. sylvestris*. North of the Black Sea and somewhat further eastwards grows a similar taxon reported to be annual-biennial, *Rorippa brachycarpa* (C. A. Mey.) Hayek, cf. p. 13. With this group of species should be mentioned also a taxon morphologically strangely intermediate between *R. sylvestris* and *R. amphibia*, described by Boissier & Hausknecht (Boissier 1888) as *Nasturtium kurdicum* and collected a few times at mountain rivers or brooks in S. Kurdistan.

Since all these species, as well as *R. sylvestris* itself in E. Europe and Asia are very incompletely known, their interrelationships cannot be outlined. But since the Pontic region constitutes a center of diversity for taxa showing a general resemblance to *R. sylvestris*, there is some reason to suspect this species to have originated in this area.

Taxonomic conclusions

Being known only as polyploid *R. sylvestris* is probably of allopolyploid origin, but the putative parental taxa cannot be imagined. Nor can any clear picture be given of the evolutionary process within the species *R. sylvestris* itself. The richness in dissimilar biotypes already at the tetraploid level might well result from interspecific crosses, certain segregational products of which have succeeded in building up clonal populations. Crosses with other *R. sylvestris* clones would efficiently contribute to increased variation.

It seems reasonable to assume within *R. sylvestris* also a selection of biotypes specially adapted as colonizers of cultivated ground, for which a strong ability of vegetative propagation and regeneration would be essential, but where reduced fertility is of minor importance. Not least the often vigorous hexaploid clones

might have originated in connexion with human activity. Since the hexaploids form a very variable group, where certain clones show a much stronger resemblance to certain tetraploids than to other hexaploids (e.g. J 401 to J 441), hexaploid clones have probably arisen a number of times from various tetraploids, perhaps by means of unreduced gametes. The pentaploids, which are rare at least in Scandinavia, are most certainly the result of a cross between tetra- and hexaploids, which assumption is supported by the facility to produce pentaploids this way experimentally (cf. Ch. 5). The rarity of pentaploids may account for the lack of finds of spontaneous aneuploids, which in crossing experiments were chiefly derived by means of pentaploids. The usually reduced fertility of the aneuploids would be no serious hindrance to their establishment as weeds (cf. above), and at least under the conditions free from competition prevailing under cultivation many aneuploid clones showed good ability for vegetative propagation (cf. also pp. 41, 127).

The taxonomic implication of the statements made above would doubtless be to maintain *R. sylvestris* as one single, variable species, whose circumscription against a number of taxa of S. E. Europe and the Near East is still uncertain. No infraspecific subdivision according to cytotypes is justified here. There may be good reason, however, to discern ecologically and morphologically specialized populations, as ssp. *kerneri* that have gained some distribution of their own.

Distributional History in Scandinavia

In Scandinavia *R. sylvestris* is nowadays mostly found as a weed. Occurrences in fairly natural vegetation are chiefly restricted to very limited regions. From herbarium material and literature reports one obtains a clear view that *R. sylvestris* has widened its distributional area considerably in recent times, a matter discussed for Denmark by Pedersen (1958).

For various reasons it was thought to be of interest to perform a rather detailed investigation of the spread of *R. sylvestris* during the time possible to survey. Firstly it would be possible to see if the great variability of the species could to some extent be traced back to different times and modes of introduction for various groups of biotypes. Secondly it would throw further light upon the question as to whether certain forms of the species have specialized ecological preferences, and particularly upon the role of the species in natural vegetation. The species was considered at least partly indigenous by e.g. Hård av Segerstad (1924), Sterner (1938) and Pedersen (1958). Thirdly, it might be of some general interest in increasing the knowledge of the rapidly changing flora of modern times. For a group of anthropochorous species their history of introduction and spread in Sweden and Denmark was clarified by Hylander (1943*a*, *b*). For a further number of anthropochores local but very detailed accounts of their modern history exist (cf. e.g.

Erkamo 1944, 1952, Pettersson 1958, Saarisalo-Taubert 1963). For most of the antropochores which since the 17th century have invaded the area (neosynanthropes, cf. Hylander 1953) or considerably widened their distribution no data of the lapse of dispersal have been gathered.

For *R. sylvestris* the historical evidence consists of herbarium specimens and literature reports. A circumstance advantageous for *R. sylvestris* in contrast to many other anthropochores, is the fact that it neither has been nor has become in any part of the region a common species escaping the botanists' notations. Therefore the sources would be impaired by an error of comparable size over the whole region.

In a map (Fig. 13) the material is presented after being grouped into a number of categories. All Scandinavian finds of the species listed in App. 4 are included in the map. A number of literature reports for which no contemporaneous nor later confirmations exist in the herbaria, and which for one reason or another seem doubtful were omitted. With respect to the date of the earliest find known from a place the material was divided into three classes. The first class includes all finds before 1875, the second those from 1875 to 1915 (these years included), and the last those after 1915. Though there are many reports already from the 1830-ies to the 1850-ies, not until the 1870-ies is there so comprehensive a material as to give an approximate picture of the actual distribution for the whole of Scandinavia at that time. Then the more cultivated regions, to which *R. sylvestris* is bound, were at least superficially known floristically and a series of provincial floras had been issued. The period from 1875 to 1915 was a time of intense floristic exploration and it is plausible that *R. sylvestris* as a "rare" species was the object of the collectors' interest in quite another degree than e.g. *R. palustris*. In fact, a greater uncertainty should be supposed for the period after 1915, when the species is becoming commoner at the same time as the floristic interest is decreasing. Hence there are probably a great number of modern localities which have not been recorded. App. 4 gives the actual year for each earliest find. There references are also made to the sources. The local area of dispersal for which only one symbol stands in the map was taken quite arbitrarily somewhat larger than the area covered by a single symbol. In some places the species has apparently become rarer or disappeared in recent times (cf. below), and therefore the years of later records from a place are also given in App. 4.

I have also attempted a distinction between occurrences in fairly natural vegetation (i.e. shores) and those in ground under strong human influence. In most sheets or literature reports there are clear indications of the kind of growth place, but also the finds without this information are included in the map in order to give as complete a picture of distribution as possible. In many cases there is no indication of growth-place in the first find, but the information given by later finds was considered possible to employ. Often both the main types of growth-places are

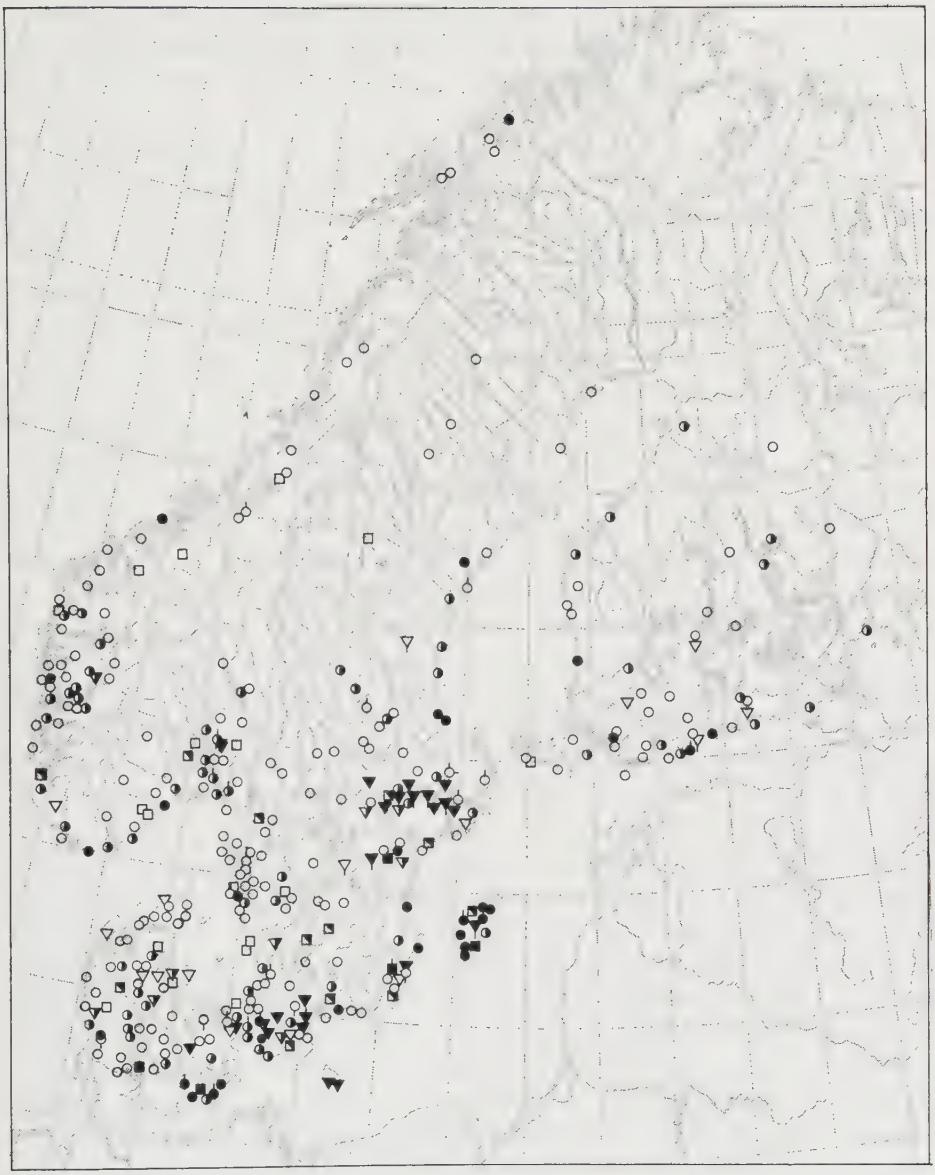

Fig. 13. *R. sylvestris*. Map of the *distributional history*, *habitat* and clones with known *chromosome number* in Scandinavia. Filled symbols = first find before 1875; half-filled symbols = first find between 1875 and 1915. Open symbols = first find after 1915 (cf. text). Triangles = occurrences on shores etc.; circles = occurrences as weeds; squares = type of habitat unknown (cf. text). Symbols with line downwards = tetraploids, with horizontal line = pentaploids, with line upwards = hexaploids.

reported from one place, which may be due to apophytic or neophytic behaviour of the plant. It may be due also to the occurrence of various forms of the species of various age at the place. Such distinctions cannot be shown in the map, but App. 4 will give some information on this matter.

Under finds in "natural" vegetation are grouped those on shores of lakes and rivers. Also finds at human constructions like bridges, landings, and walls are included, since they might be due to hemerophily of an otherwise spontaneous population. In all other cases the species is recorded as a complete anthropochore, a weed (examples of growth-places, cf. App. 4). Specimens collected in towns have been grouped as anthropochores, even if no further indication of the habitat was given.

The map shows that before 1875 the species was restricted on the one hand to a number of harbours, on the other to a few regions (Lolland, Falster, Bornholm, S. W. and E. Skåne, Öland, Gotland, Central Östergötland and the Mälar-Hjälmar region), where it had partly a spontaneous character. The first, but not fully reliable Swedish find is from Göteborg (Bromelius 1694 acc. to Nordstedt 1920). Linnaeus (1755) did not know the species from Sweden by personal experience, but cited Rosén (1749), who knew it from rivers in Skåne. It was reported by the 19th century authors from e.g. the rivers Segeå, Höjeå, Helgeå (cf. E. Fries 1835, Areschoug 1881), and even from sandy places near the sea at Arlöv (Wahlenberg 1824). The Bornholm finds are from small rivers in the south-western part, where it was said to be rather frequent (Bergstedt 1883). In Östergötland it was evidently regarded as rather scarce and chiefly found at L. Roxen (Kindberg 1901). All specimens from these localities are of slender habit, have rather short petals etc., approaching the forms typical of the Mälar-region (cf. p. 95).

After 1900 there are, however, very few records of the species from "natural" localities in Skåne, Bornholm and Östergötland. Visiting a number of places for earlier finds in all three provinces, I found only at L. Roxen a clone (J 620) with obvious connexion with the old records, both morphologically and ecologically, though in its present growth-place the species had a clearly apophytic character. Also from A. Larsen (1956) it is evident that the species has not been found at the small rivers in Bornholm after 1900. Nor has the intense floristic exploration of Skåne led to more than a few finds at rivers or lakes, some of which, however, are morphologically aberrant from the old river populations and probably introductions of recent date (e.g. J 1235, 1307, cf. p. 126). Along the Scanian rivers mentioned above it is today difficult to see even a suitable natural growth-place for the species. But the early reports only give the habitat as "shores" etc., and hence it cannot be excluded that the *R. sylvestris* populations were bound to places that because of human activity were devoid of competing vegetation, e.g. bridges, landings, which are now in a high degree provided with stony embankments if still in use. The very unstable character of these populations, which have obviously

not obtained a real foothold in the environment and rapidly decreased when conditions changed, makes their indigenity highly doubtful.

In Scandinavia it is only at L. Mälaren that the species may be regularly found under fairly natural conditions over a wider area. As remarked by Almquist (1965) *R. sylvestris*, known only as a freshwater species and nowhere spread on shores of the Baltic, can hardly be older at L. Mälaren than the lake itself. The formation of this lake from a former bay of the Baltic has been a gradual process, where the sounds to the open sea because of the land uplift have become narrower and fewer and finally closed (cf. e.g. Florin 1957). The final closure at Stockholm would have occurred about 1200 A.D. (Granlund 1930, Lundqvist 1930). Long before that, perhaps during a millenium, conditions suitable for freshwater macrophytes may have existed because of the gradual transition to freshwater in the bay. No general account of the history of L. Mälaren exists, however. Whether spread by seeds or by vegetative fragments introduction through shipping—perhaps while the passage still was free from the Baltic—seems more probable than spontaneous immigration, since as a shore-plant the species is in this part of Sweden almost confined to L. Mälaren. *R. sylvestris* should therefore be considered as a probable neophyte at that lake. The few specimens from L. Hjälmaren are morphologically close to the Mälar-populations, and might well have been spread there by ships from L. Mälaren, as have certainly the specimens reported from the Strömsholm Canal (Västmanland). Shipping may also account for a number of finds in Östergötland, viz. those from waters connected by the Göta Canal, but floristic evidence for the region from time before the Canal construction is lacking.

From Lolland-Falster and Gotland *R. sylvestris* is also known since the early 19th century, but there are very few reports from rivers or lakes. Most finds from Lolland-Falster are from roads and similar places, and the species is here certainly originally an anthropochore. For Gotland the plant was reported by Wahlenberg (1821) to grow at roads in many places. It was early known also from several harbours, e.g. from Visby already before 1837 (Säve 1837), and the collections there from 1863 till the present time mostly consist of an easily recognizable form, obviously belonging to one and the same clone (cf. p. 94). This clone has not been found elsewhere. There seems to have been different biotypes collected in each of the Gotlandic harbours. We can here obviously trace repeated introductions, which have in most cases probably not lead to any wider spreading of the plant. The plant is now probably extinct in most harbours mentioned in App. 4, since I searched it in vain in 1961–1962. But it seems probable that the inland localities at roads emanate from harbours, and anthropochorous origin might thus be suspected also for the few localities at rivers (Dalhemsån; cf. Johansson 1897, J 900).

From easternmost Fennoscandia (Karelia olonetsensis and K. pomorica occidentalis) a few alluvial occurrences are known that are probably outposts of the

population at North Russian rivers, but nevertheless may result from anthropochorous dispersal (cf. p. 96, Fagerström & Luther 1946).

For the local, single or repeated finds on shores, both from old (as Sjælland, Öland, Oslo) and more recent times (e.g. single lakes in Halland, Värmland, Hordaland) a quite local naturalization seems to be the most convincing explanation.

All evidence presented as well as deliberations on dispersal biology (Ch. 4) speak in favour of an anthropochorous introduction of *R. sylvestris* to all parts of its Nordic distribution area, though secondary spontaneous dispersal may sometimes have been of importance. The age of the plant may, of course, in certain regions go much further back than is possible to survey.

As already exemplified on Gotland *R. sylvestris* was in the 19th century mostly known from harbours, which would have been gateways for further spread and the source of still existing populations (cf. Hjelt 1904–1906, Saarisalo-Taubert 1963, Mäkinen & Laine 1962). These authors report the species from a number of harbour towns as initially a ballast plant and so it grew also in some Swedish harbours (cf. App. 4). In Norway most old finds of *R. sylvestris* are from places known to have had a rich ballast flora (cf. Ouren 1959). With the disappearance of this type of localities and with the construction of modern harbours the species is probably mostly extinct in such places, though it may still grow as a weed in the adjacent town (cf. Saarisalo-Taubert 1963, p. 124). Under special conditions the species has also recently been introduced to harbours, e.g. as a German polemochore (definition in Mannerkorpi 1944–45) in the Finnish harbours of Kaskö and Kristinestad (Luther 1948–49) and with foreign troops it was also spread to inner parts of Finland (Fagerström 1958).

Particularly after 1915, however, the number of inland finds of the species have increased markedly. The growth-places are very often gardens, otherwise roadsides and courtyards (even rather dry places), ditches, embankments and there are finally some neophytic occurrences at rivers and lakes (cf. App. 4). Since the recent finds in many cases clearly represent forms not previously known from the region, the earlier occurrences have probably not played a significant role as centres for this spread. In the Mälar provinces, for instance, *R. sylvestris* is an infrequent weed, and the Mälar population has not spread considerably from the shores. The weeds existing in the area belong to other biotypes and probably mostly even to another cytotype (cf. Fig. 13), and must therefore be fresh introductions. In some other floristically well-known—and therefore comparable—regions as S. Bohuslän with the Göteborg area or N. Jutland, the species is, on the other hand, a rather frequent weed. From there no early localities are known besides the one in Göteborg. This city might have served as a centre of dispersal. In the sandy districts of N. Jutland it has expanded rapidly (cf. Pedersen 1958). In Skåne the plant is in modern weedy occurrences represented by clones differing from the older ones at rivers.

The limited possibilities of formation of new biotypes within large parts of the Nordic distribution area were discussed in Ch. 4, and from this circumstance it seems most probable that the majority of clones occurring as weeds were introduced from regions where *R. sylvestris* is more frequent. As emphasized above it is difficult to trace the origin by means of morphological comparisons. It was demonstrated by Ouren (1959) that the bulk of Norwegian ballast emanated from Western Europe, notably Great Britain, Belgium and the Netherlands. Since *R. sylvestris* is particularly frequent in the last-mentioned countries (Lawalrée 1955–57, Heukels & v. Ooststroom 1956) introductions from there would have been of importance, at least for Norway, in the form of vegetative parts or as seeds, since seed-production is of a much greater importance in regions with a dense *R. sylvestris* population (cf. p. 36). In a few cases *R. sylvestris* was found at mills (Hanssen & Nordhagen 1930, cf. also App. 4), which clearly indicates seed dispersal.

For the many recent discoveries of the species, not least in inland regions the concentration of finds to gardens suggests transports of diaspores with garden soil. Primarily these clones would have been brought to the Nordic region with soil accompanying imported garden plants. One may suppose that many clones emanate from Belgium and the Netherlands also in this case. Confirmation on this point was attempted through studies of Netherlandic herbarium material, but they gave no clear results.

C. *Rorippa amphibia*

In *R. amphibia*, which has a rather vast Eurasiatic distribution (cf. p. 162) the seasonal variation in relation to environment has been studied in some detail (Glück 1911, Baumann 1911, Kopecký 1965*b*; see further p. 106). These studies have also some bearing upon the understanding of the variation observed between different populations. No critical taxonomic study of the species does, however, exist for any part of its range. In regions where it hybridizes with *R. sylvestris* the variation is often large. Already Linnaeus (1753) discerned three varieties chiefly according to their various types of leaves, but he obviously included both hybrids and our *R. palustris* in his polymorphic species, called *Sisymbrium amphibium* (cf. Ch. 7). Within the species as circumscribed today notable variation has been reported in three different respects, viz. as to cytotype, leaf-shape and pod-shape.

Distribution of the cytotypes

Only from part of the area of *R. amphibia* we have some knowledge of the distribution of the two cytotypes (cf. Table I), viz. Scandinavia, the British Isles and to some degree the westernmost part of Continental Europe (cf. Fig. 14).

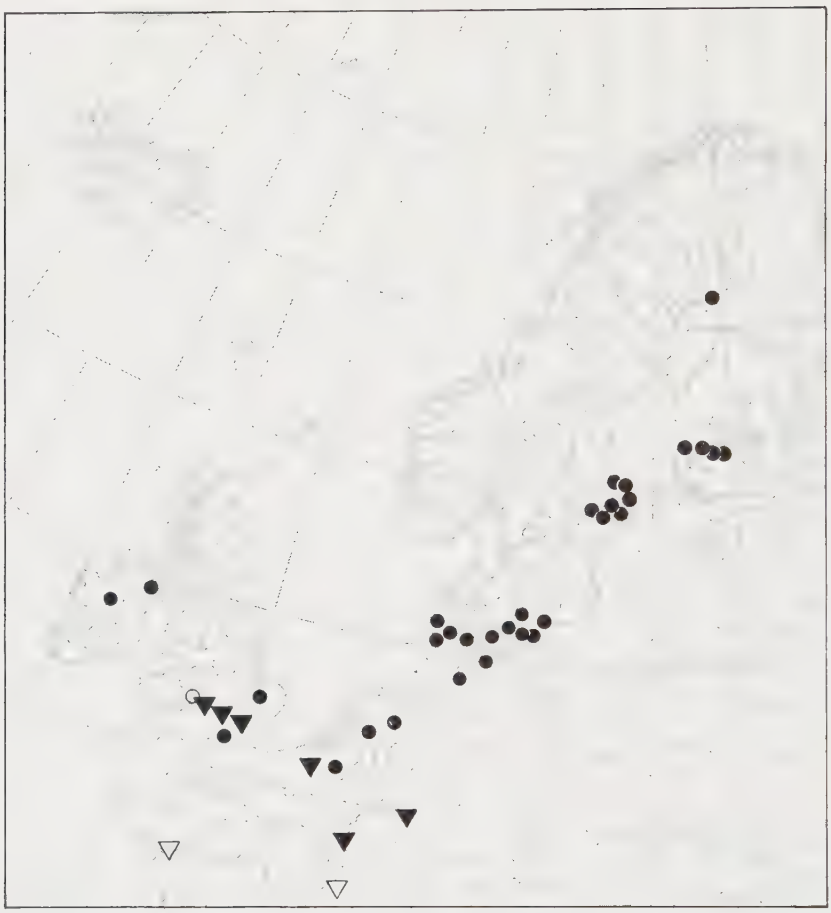

Fig. 14. *R. amphibia*. Localities from which chromosome numbers have been verified. ▼ = diploids; ▽ = diploids, position not exactly known; ● = tetraploids; ○ = tetraploid *R. amphibia* × *sylvestris* very close to *R. amphibia*. Many symbols, esp. in Sweden, cover many localities close to each other. (The locality of a diploid from Portugal falls outside the map.)

Within this region the tetraploid dominates. In Scandinavia (Finland, Sweden and Denmark) only tetraploids were found. Since a comparatively large material was investigated from the three important Nordic part areas (cf. p. 109) of the species, it seems very unlikely that any diploids should exist there.

The British Isles house both cytotypes. The diploid is known only from along the Thames but seems there to constitute the whole population. The remaining determinations, some few from S. England and Ireland have turned out to be tetraploid.

From the Continent some tetraploids are known from Schleswig-Holstein south-

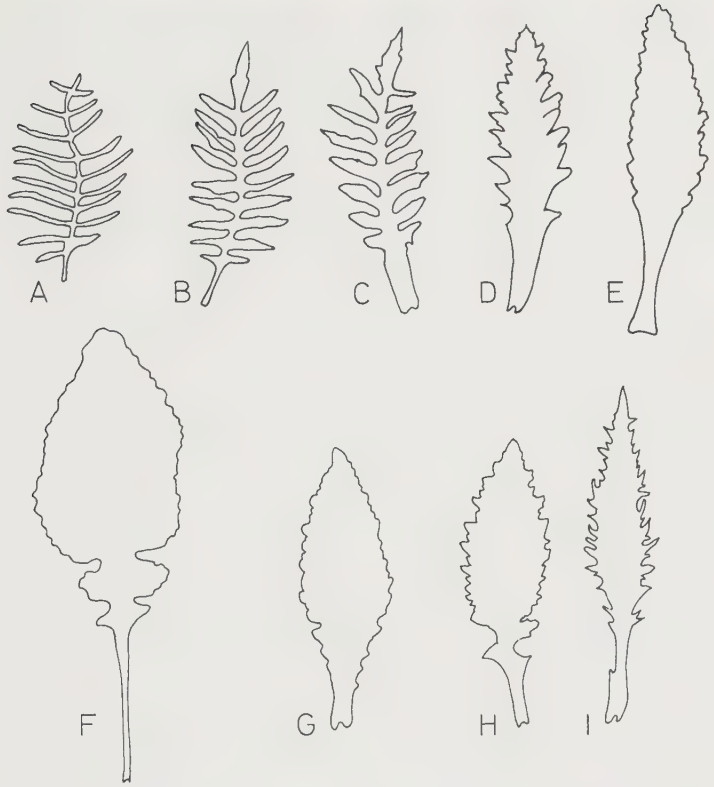

Fig. 15. Leaves of *R. amphibia*. A–E: series of cauline leaves from near the base (A) to the middle of the stem (E), (J 409). F: lyrate leaf from a basal rosette, (J 1390). G: leaf from the middle part of the stem in a British diploid, (J 1166). H–I: leaves from the middle part of stems in an Irish tetraploid, (J 1188). $\frac{1}{2}\times$.

wards to Belgium (Wulff 1939, J 1140, 1142, 1146) and seem thus to be connected with the S. Scandinavian population. Plants from six localities farther southwards, in Belgium, Germany, France and Portugal (J 252, 952, 1147, 1320, 1462, 1580) were, on the contrary, all diploid. The British and Continental material is of course too small to reflect with any accuracy the real distribution of the cytotypes.

Variation in leaf-shape

The first leaves to arise on the young shoots after overwintering or sometimes already late in the autumn are deeply pinnatisect with numerous lateral segments. Such leaves are formed irrespective of whether the shoot is terrestrial or aquatic, but in the latter case the leaves become larger and pronouncedly pectinate, sometimes with almost capillate segments (Fig. 15 A). The sequent leaves become less and less lobate and rather soon the well-known, nearly entire leaves are formed (Fig. 15, B–E). Under natural conditions the pinnatisect-lobate leaves are sub-

merged during the summer and they usually soon disappear, as they do in the terrestrial cultivation. Lyrate shape is generally found in the rosette leaves, which are distinctly petiolate (Fig. 15 F). In prostrate-decumbent stems rosettes of such leaves are found on lateral branchlets. More rarely petiolate and lyrate leaves may occur along ascending-erect stems.

There is accordingly a kind of heterophylly in *R. amphibia* but without sharp limits between the leaf types. Though I have not seen all types of leaves in all of my cultivated material, nothing contradicts that the leaf-variation described occurs in all *R. amphibia*.

The variable leaf-shape has been paid fairly much attention to, notably by Glück (1911), Baumann (1911) and Kopecký (1965*b*), all of whom put it in relation to the environment. Glück regarded his material, chiefly studied in cultivation, to consist of two varieties, one of which only (var. *variifolium* DC.) showed divided primary leaves while the other (var. *auriculatum* DC.) developed lyrate primary leaves. Baumann (op. cit.) remarked that his material, studied in the field, was not possible to assort into two groups, but tended to var. *variifolium* in the spring, to var. *auriculatum* with lyrate leaves in rosettes in the summer and autumn. The studies by Kopecký (op. cit.) of the variation of *R. amphibia* throughout the year at a Bohemian river show also a seasonal variation, though he does not mention whether leaf-rosettes are produced. Kopecký's suggestion that the seasonal leaf-variation would be a genetically fixed response to the annual water-level cycle seems premature, however, since *R. amphibia* grows in many places where the water-level varies in other ways or hardly at all. Here as in other helophytic plants (e.g. *Sium latifolium* L.) the leaves differ between the basal, usually inundated, and the upper parts of the plant.

The whole Irish population of *R. amphibia* (J 1175, 1188, herb. mtrl) seems to have deeply serrate upper cauline leaves. This might well be a character intrograded from *R. sylvestris*, especially as its pod-shape also indicates such a situation.

The variable leaf-shape was described already in the beginning of the 19th century. De Candolle (1821, 1824) discerned three varieties under *Nasturtium amphibium*, the two mentioned above, and var. *indivisum*. I have not seen the authentic specimens, but there is no indication that the leaf-variation upon which they are based is of taxonomic importance. Var. *indivisum* was evidently applied to specimens where only the normal cauline leaves were seen. To var. *variifolium* at least some authors after De Candolle, e.g. Reichenbach (1837–38), to judge from his plates, attributed hybrid specimens close to pure *R. amphibia*. Also Nordic floras from the 19th century (e.g. Hartman 1879) record some of these varieties.

Variation in pod-shape

In spite of conspicuous variation the pod-shape has not been paid attention to in the same degree as the leaves. This is partly due to the scarcity of fertile and well

developed pods in the herbarium material from many regions (cf. p. 36 f.). It was treated in some French floras (Godron 1843, Grenier & Godron 1848, Rouy & Foucaud 1895). In the first-mentioned work two varieties were recognized, viz. var. *rotundisiliqua* and var. *longisiliqua*. Rechinger (1960) revived the former name for a specimen from Syria (Haradjian No. 4161) with rounded, but not fully ripe pods, at least not in the specimens present in K and E. Also Russian authors have observed this variation (Ledebour 1842, Busch 1913–31). The different shapes depend mainly upon the varying lengths of the pods, in Nordic and British material 2.5–5.3 mm (mean values in the specimens). The width is rather constant (about 2.0–2.5 mm). Of course it is tempting to interpret the long pods as a result of introgression from *R. sylvestris*, e.g. in some clones from Skåne (J 1096, 1099) and Ireland (J 1175, 1188), perhaps also in some other tetraploids (J 1142, 1146). But the long pods occurring in some diploids cannot have arisen that way (cf. below).

An important feature of *R. amphibia* is its long style, well set off from the pod and of good use in evaluation of hybrids (cf. p. 113). The style-lengths vary considerably between the *R. amphibia* clones, from 1.0 to about 2.5 mm, whereas the amplitude in one and the same specimen may reach about ± 20 %. The variation seems not to be correlated with that of any other characters and to be present in each of the N. W. European areas of the species. Other European material seems to reflect a similar state.

Relations between cytotypes and morphology

The diploid cytotype from the Thames valley consists probably of several clones but is morphologically rather uniform and somewhat deviating from British and Scandinavian tetraploids. The Thames plants have usually auriculate leaves, often with broad mid-veins and a tendency to petioles. They have markedly pubescent young shoots, styles of short to medium length and comparatively long pods, from 4 to 6 mm (in single pods). Still longer pods were measured in herbarium specimens from the Thames. The pods are mostly of such a length that is found among tetraploids only where introgression from *R. sylvestris* can be suspected. These features taken together make specimens from the Thames valley fairly well recognizable within N. W. European material.

The few Continental diploids examined are rather unlike the Thames plants. None has petiolate leaves, nor auricles, but such may be absent from British diploids, too. A French specimen (J 252) has a sparse pubescence and very short pods, a Belgium one (J 1147) shows similar pubescence and pods of medium length, while a Portuguese plant (J 952) has pubescent shoots and rather long pods, which, however, have an extremely long (c. 1.5 mm) sterile portion next to the point of attachment. This feature seems to be constant in *R. amphibia* from the restricted Portuguese distribution area, as judged from herbarium specimens seen. Already from these few and scattered samples it seems probable that the diploids cover a

range of morphological variation comparable and perhaps parallel to that displayed by the tetraploids. Pubescence of the young shoots, for example, occurs in tetraploid populations, too.

In flower-size and seed-coat structure there is no important variation in *R. amphibia* at all, and no trends to a difference between the cytotypes. There seems not to be any qualitative distinguishing features present like the ones separating *R. islandica* and *R. palustris*. But locally and because of vegetative propagation abnormal features may prevail throughout an isolated *R. amphibia* population. One example is probably the pod-shape referred to above for Portuguese specimens, but many other, more or less drastic anomalies are known, particularly in reproductive organs, and in many cases they cause partial or complete sterility.

The fertility of the pollen is very variable in *R. amphibia*, ranging from 0–95 % of stainable grains (in most clones 30–70 %). The tendency seems to be the same in the two cytotypes, but all clones with less than 20 % of stainable grains were tetraploid.

As seen from Table II there is a difference in pollen-size between the cytotypes, which is of about the same size as that found between *R. islandica* and *R. palustris*. Here, too, the grains of the diploids are almost exclusively tricolpate, while some few per cent of tetracolpate grains may be found in the tetraploids. The cytotype of a specimen may be estimated with a certain degree of probability from its pollen-size, and this seems here to be the sole possibility of deducing the cytotype from morphology.

The total failure to produce triploid progeny (cf. p. 44) indicates the presence of a strong sterility barrier between the cytotypes. I have not found the two cytotypes growing in the same locality or water system, but such a situation may exist e.g. in Belgium or England to judge from present knowledge. *R. amphibia* is obviously another case where cytotypes cannot be used in practical taxonomy. In spite of the existence of two genetically isolated cytotypes the species cannot possibly be split at any taxonomic level by means of the chromosome numbers. There remains much to be done, however, before the morphological, geographical and genetical interrelationships of the cytotypes can be considered sufficiently known.

Several similar examples have been brought to light in later years. Well documented cases where diploids and tetraploids seem to be impossible to separate taxonomically are e.g. *Anthoxanthum odoratum* L. (I. Hedberg 1961, 1967) and *Cardamine amara* L. (Habeler 1963). In both cases the cytotypes are only to a minor extent sympatric and might once have been isolated from each other geographically for a considerable time. In *Anthoxanthum* there are clear tendencies to morphological and not least ecological differences at least over large parts of the area, while in *Cardamine amara* there is even in pollen-size only a weak tendency to a difference between the cytotypes.

Strict autopolyploidy is not considered by Stebbins (1950) a common evolutionary way in spontaneous populations, and only few clear examples are cited, while allopolyploidy or segmental allopolyploidy would be of far greater importance. In *R. amphibia* the situation seems to be known well enough to exclude an origin of the tetraploid from two morphologically well distinct diploids. Tetraploids may have arisen repeatedly in various other ways and the effective vegetative propagation should have facilitated their establishment. Time would have been sufficient for selection against the initial high sterility expected.

Remarks on the Nordic distribution

The south Swedish–Danish area is an outpost of the rich occurrences in the North German lowland (Christiansen 1953, Hegi 1958–63) with connexions via Schleswig–S. Jutland. The remaining Nordic areas are rather isolated. Only in two is the plant an important constituent of the aquatic vegetation, viz. one consisting of Lake Mälaren and many waters in Central and Northern Uppland (Sweden), the other in the Kumo River system (Finland). It has also been collected in E. Småland (Klm: e.g. Hossmo, 1887 H. Simmons, UPS; Hagby, 1895 T. Freidenfelt, UPS and 1919 R. Sterner, UPS; Döderhult, 1928 R. Sterner, UPS), the central plain in Östergötland (e.g. Linköping, v. Goës, UPS; cf. also Kindberg 1901; no collections from later years), N. Halland (Släp, 1907 Persson, UPS) and the Göta River valley (Vg: Nödinge, 1947 C. Blom, GB, S). Unverified but plausible records occur from Västergötland, near Vänersborg (Sahlén 1854). A sheet only marked herb. Montinii 1782 "in Hallandia" exists in S (cf. also Ahlfvengren 1924). A surprising outpost was found recently near the mouth of the Torne River (Ostrobottnia borealis, Finland) (Hylander 1960). There are also some finds in easternmost Fennoscandia (Karelia onegensis and K. olonetsensis, at Lake Onega and some adjacent smaller lakes; Hjelt 1904–06, Fagerström 1945), which are probable outposts of a rather continuous Russian distribution area.

Obviously erroneous are the reports from the Swedish provinces Öland (Sjöstrand 1863) and Värmland (Larsson 1868), which have never been verified (cf. Sterner 1938 and Hård av Segerstad 1952 resp.) and from Västergötland, Mariestad (Hasselrot 1967), which actually concerns *R. austriaca*. Some reports of weedy occurrences far from spontaneous ones have turned out to be *R. austriaca* or *R. austriaca* × *sylvestris* (cf. Fagerström 1939–40, 1942; Lid 1963 as to most of the Norwegian records). Two ballast localities (Akh: Oslo, Grönlien, 1883 Fridtz, O a.o.; AuAgd: Lyngör, 1903 Lynge, O) are the only ones verified from Norway. A critical survey of dubious old finds in Finland was given by Hjelt (1904–06). He reported also two finds from Karelia australis, one without further indications of the locality, the other from a railway near Viborg. The corresponding sheets (in H) are both dubious and should not be regarded as verifying the existence of *R. amphibia* in Karelia australis.

R. amphibia is a clearly eutrophic species (cf. Hård av Segerstad 1924) but the disjunct Nordic distribution only partly coincides with the boundaries of eutrophic regions. Such a coincidence seems clear in Jutland, where *R. amphibia* avoids the more oligotrophic northern parts, and in southernmost Sweden, where it is common in the eutrophic parts of Skåne but absent from the oligotrophic highland. Edaphic conditions seem here more probable to put the distributional limits than climatic ones (cf. Pedersen 1958 and Hård av Segerstad 1924 resp.), since the species grows constantly already in Scandinavia much farther to the north. Samuelsson (1934) placed *R. amphibia* in a group of South Scandinavian aquatic plants, whose borders in Sweden approximately coincide with the northern limit of *Quercus robur* L. ("limes norrlandicus", cf. M. Fries 1948), and which reach S. Finland. *R. amphibia* has, however, in Central Scandinavia a much more restricted distribution than at least the other helophytes (except *Cladium mariscus* (L.) R. Br.) in Samuelsson's group (*Acorus calamus* L. (originally introduced), *Rumex hydrolapathum* Huds., *Sium latifolium* L.), and than a number of other eutrophic plants not treated by Samuelsson (e.g. *Carex pseudocyperus* L., *C. riparia* Curt. and *Veronica anagallis-aquatica* L.) as well. Also *Oenanthe aquatica* (L.) Poir., which reaches somewhat farther northwards than the species mentioned is a similar example. Like these species *R. amphibia* should be able to grow e.g. in many more parts of Östergötland, in Västergötland, Närke and inner Södermanland.

In the Mälar region *R. amphibia* is outside L. Mälaren itself confined to Upplandic lakes and rivers.[1] Some of these localities lie at waters that formerly were bays or straits of L. Mälaren (cf. p. 101). But the species is frequent in a number of water systems running towards the Baltic, from lakes situated at about 20 m s.m. to those very recently and even incompletely isolated from the sea (cf. Willén 1962). It reaches still higher e.g. in L. Vendelsjön (24 m) and L. Tämnaren (c. 40 m). The actual part of Uppland is, particularly towards the north and in contrast to the other provinces around L. Mälaren, covered by a moraine rich in lime (cf. Magnusson *et al.* 1963), which would be favourable but hardly decisive for the occurrence of this species. Like *R. sylvestris R. amphibia* cannot have grown at the sea-gulf preceding L. Mälaren as long as brackish water prevailed.

The isolated Uppland–Mälaren area makes introduction there through shipping possible also for this species, and it might have been spread to now isolated Upplandic lakes through the net of fairways that connected central Uppland with the Baltic during the Iron Age (cf. e.g. Sundqvist 1953, Ambrosiani 1961). It is, however, difficult to connect the present Upplandic distribution with the

[1] Exceptions are three specimens from Srm: shore of R. Eskilstunaån, and Torshälla at R. Nybyån, both 1841 Lindblad (S), and Torshälla, 1899, v. Porat (UPS).

fairways known. Also some of the lakes in eastern Uppland where *R. amphibia* grows (e.g. L. Erken and L. Närdingen) were in medieval times still possible to reach with ships from the Baltic (Wallén 1911). A good example that *R. amphibia* can be spread long distances with ships is its occurrence in Canada at the St. Lawrence River (Marie-Victorin 1930) and another example is probably its occurrence at the Göta River (cf. above). The occurrences at Upplandic lakes on rather high levels are more difficult to explain in such a way, however, although boat passages connected with the lower fairways might have existed. It can only be concluded that *R. amphibia* in Central Sweden shows a distributional picture, whose borders are probably not determined by environmental but rather by historical causes.

In the Kumo River system *R. amphibia* is frequent in many parts (for details cf. Hjelt 1904–06, Häyrén 1909, Pohjala 1934, Suominen 1962, Jalas 1965) and is known since the earliest floristic records were made in the region. Anthropochorous introduction followed by dispersal over a vast area is possible here, too, but there are no special circumstances supporting such a theory, but for the fact that the Kumo River system has for long times been an important trade way and centre of commerce (cf. Jaakkola 1933*a*, p. 169; maps in Jaakkola 1933*b*, Nordman 1933). Edaphic conditions may here put limits to the species, since the eutrophic south-western part of Finland reaches the Kumo River and some of its source-lakes (cf. map p. 36 in Valovirta & Segerstråle 1956), which are by far the most important waters of that region. Some of the aquatic species mentioned above are in Finland (besides the Ladoga region) mainly found in the south-western part, but in contrast to *R. amphibia* also outside (to the south of) the Kumo River system. The *R. amphibia* population there obviously consists of a number of clones, since it sets seeds (cf. p. 36).

The isolated find in the Torne River, about 500 km N. of the nearest occurrences (Kumo R.) was assumed by Julin & Pekkari (1965) to be a case of long-distance dispersal by human agencies. As discussed in p. 130 it may have been brought there together with its hybrid with *R. sylvestris*, which grows in the same place.

D. Interspecific Hybrids

During the 19th and the early part of the 20th century *Rorippa* hybrids were studied, as mentioned in Ch. 1, particularly by Central European botanists. This interest led to the naming of numerous derivatives within these often fertile hybrids (cf. p. 151) both as species and as infraspecific taxa. The description of new taxa was most intense in the Austrian Empire (e.g. Tausch 1840, Borbás 1879*a*, Beck 1890–93, Zapałowicz 1912, Prodan 1919), but also Swiss, French and German botanists brought a share of names (Bergeret 1784, Wallroth 1822,

1840, Reichenbach 1830–32, Godron 1854, Gremli 1867, Zschacke 1901). From Britain and Scandinavia only few names were given to *Rorippa* hybrids. Most important is *Sisymbrium anceps*, described by Wahlenberg (1820) from near Uppsala. This paucity of course depends upon the much more local occurrences of the hybrids as well as of the parent species in the latter regions (cf. below).

Rather early some authors suggested a hybrid nature for a number of the taxa described (Reichenbach 1830–32, Neilreich 1852). Towards the end of the 19th century such opinions became widespread. The most comprehensive attempt to survey the hybridizing *Rorippas* was made by Borbás in some works, especially 1879*a*. There the morphology of a number of forms described and specimens distributed in exsiccata under diverse names were discussed and interpreted as hybrids. A few forms, among others *Rorippa anceps* (Wg) Rchb., were interpreted as intermediate but independent species (Borbás op. cit. and 1882; see further below), for which sometimes the obscure term "nicht hybride Zwischenform" or "Zwischenart" was later used (e.g. Schinz & Thellung 1909, 1913). However, a rich number of new names for what is certainly hybrid derivatives also resulted from Borbás's works. Fröhlich (1914) performed a critical study, in which the hybrid nature of a series of supposed species is documented. Also in the mainly ecological work by Baumann (1911) *Rorippa* hybrids are taxonomically discussed (see below p. 133). A survey of the names of *Rorippa* hybrids with their current binary names is to be found in Janchen (1956–60). In the recent Rumanian flora (Săvulescu *et al.* 1955) a great many *Rorippa* hybrids are treated and illustrated, but it is doubtful whether all these identifications on apparently only morphological and distributional grounds will hold good. Previous Scandinavian discussions on *Rorippa* hybrids will be referred to below.

Except for some cases of special relevance no attempts will be made here to clarify the identity of the various hybrid derivatives described as independent taxa. The following account is based upon studies of spontaneous hybrid material in the field and in cultivation (see Ch. 1), and of herbarium specimens from Scandinavia and Britain. The rich amount of biotypes represented in Continental herbaria can hardly be successfully evaluated without field studies of populations in Central Europe together with cytological investigations. The N. W. European *Rorippa* hybrids fall quite naturally into three groups, which will be treated separately: the *Rorippa amphibia* hybrids (with *R. palustris* and *R. sylvestris*), the *R. palustris* × *sylvestris* hybrids and the *R. austriaca* × *sylvestris* hybrids. Statements in the following refer, unless otherwise stated, to Nordic and British material only and are not necessarily applicable to e.g. Central European plants.

Evidence of the hybrid nature of the forms referred to these series is given in the following as well as in Ch. 5, and includes facts from morphology, distribution, behaviour in the habitat, fertility, artificial crossings, and seed progeny.

The *Rorippa amphibia* hybrids

Previous interpretations of the Nordic hybrids

The participation of *R. amphibia* in a hybrid specimen is usually easily seen, both in the field and in the herbarium. Important characters revealing this species are the tall shoots, the tendency to form pectinate basal and non-lobate upper leaves, the deflexed pedicels of ripening as well as barren pods, and the narrow styles with an average length of more than 1.2 mm. Some of these features might well characterize *R. austriaca* hybrids too, but those can usually be safely singled out by their more or less ascending, not deflexed pedicels, and their special leaf-shape (see further the key p. 154 and Figs. 21, 22). As it is thus easy to classify a specimen as derived from *R. amphibia* on the one hand, it is equally clear that the other component must be sought among species with divided leaves and longer and narrower pods. For cytological (see Ch. 2) and geographical reasons only *R. palustris* and *R. sylvestris* can be seriously considered while *R. islandica* can be excluded. No material seen could be interpreted as *R. amphibia* × *austriaca* although this hybrid is recorded for Sweden in a recent flora (Lid 1963). This hybrid also appears in Central European literature (Borbás 1879*a*, Săvulescu *et al.* 1955, Heukels & v. Ooststroom 1956), but it seems doubtful if such a hybrid exists in nature.

Discussions on Nordic *R. amphibia* hybrids have chiefly been concerned with the question as to whether they were the results of crossings with *R. palustris* or with *R. sylvestris*. The earliest Nordic report for what would be a *R. amphibia* hybrid goes back to Ehrhart (1790) and refers to a locality near Uppsala. He attributed his plant to the Linnaean variety *Sisymbrium amphibium* γ *terrestre* (cf. p. 147). Wahlenberg (1820) regarded the Uppsala population a separate species, the above-mentioned *Sisymbrium anceps*.[1] In Flora Suecica (Wahlenberg 1824) he referred also plants from Skåne to this species, now called *Nasturtium anceps* (Wg) Rchb. Under this name the species was included in Nordic literature during the middle and end of the 19th century.

Quite naturally the interpretation of *Nasturtium anceps* became the starting point and a chief topic in the discussion of *Rorippa* hybrids in Sweden. According to E. Fries (1843) discussions were held about ("fuit sermo") it being a hybrid of *Nasturtium sylvestre*, or a variety of *N. amphibium* or *N. sylvestre*, which reflects that a variable biotype material must have been studied. Pointing to the absence of *R. sylvestre* from the Uppsala region Fries (l.c.)—as he usually did—denied the hybrid theory. He referred especially to a form of *N. anceps* with petals smaller than the sepals (distributed in Herb. norm. fasc. XI, No. 36 as *N. anceps* var. *micropetalum* Fries) and pointed out its similarity to *N. palustre* (see further below

[1] Wahlenberg's description and material are discussed in the nomenclature chapter No. 7.

on this Friesian specimen). Fries was apparently the first to suggest a connexion between *N. palustre* and *N. anceps*. But he still regarded the latter a "genuine species". For an analysis of what the hybrid term meant to Fries and his time see Weimarck (1958) and Eriksson (1962, p. 398).

Borbás (1879*a*) also studied specimens of *Rorippa anceps* from near Uppsala collected by Wickström and Fries (the latter in Herb. norm. fasc. VI, No. 18) as well as a Wahlenberg specimen. This led him to consider the Uppsala *Rorippa anceps* (Wg) Rchb., as it was now called, a hybrid ("Bastard") or an intermediate form between *R. amphibia* and *R. palustris*. Borbás also cited a confirmation of his opinion from C. F. Nyman, who all the same regarded *R. anceps* as an independent species.[1] Not until the editing of Neuman's flora (1901) was the opinion of *N. anceps* as a species abandoned in a Scandinavian flora. In this work Ahlfvengren, who wrote the section on the *Cruciferae*, considered the Swedish *N. anceps* material very heterogeneous and interpreted it in part as *R. amphibia* × *palustris*, in part as *R. amphibia* × *sylvestris*. Both hybrids were said to exist in Skåne as well as in the Mälar region. Under the first mentioned designation three different *formae* were distinguished according to their similarity to the parent species.

Ahlfvengren's opinion about the two hybrids was widely followed in Scandinavia and will be referred to here. He admitted considerable difficulties in distinguishing the hybrids, but stressed that *R. amphibia* × *palustris* should always have some cauline leaves with auricles—totally absent in *R. amphibia* × *sylvestris*—and have petals about 1 mm shorter than *R. amphibia* × *sylvestris*. The cauline leaves should be more broadly and coarsely divided in *R. amphibia* × *palustris*. In no other Scandinavian or British flora is any detailed morphological treatment of these hybrids to be found.

These assumptions about the distinguishing characters made it quite natural that most of the hybrid population found e.g. in the Uppsala region, was referred to *R. amphibia* × *palustris* e.g. by Almquist (1929) an opinion to which I myself previously agreed (cf. Almquist 1965 and p. 124). Hiitonen (1947) presented an opposite meaning, as he—though without giving any clear reasons—considered Wahlenberg's *Nasturtium anceps* to be a *R. amphibia* × *sylvestris* hybrid. From other parts of the Mälar region, as well as from Skåne, Denmark and the British Isles both hybrids are reported in many recent floras (e.g. Weimarck 1963, Lid 1963, Clapham, Tutin & Warburg 1962).

Morphology of artificial hybrids

In Ch. 5 an account was given of the crossing experiments but the morphology of the F_1 progeny of the crosses of *R. amphibia* with *R. palustris* and *R. sylvestris*

[1] Borbás (l.c.) interpreted a number of Central European collections distributed under the name *Nasturtium anceps* as *R. amphibia* × *sylvestris*.

will best be treated in this connexion. The plants raised from the two *R. amphibia* × *R. palustris* crosses (J 919 × J 950, J 379 × J 471) were few and agreed in all essential features, which are listed in Table V. They will be compared with progeny of the *R. amphibia* × *R. sylvestris* cross J 361 × J 406 (cf. Table V).

The following distinctions between the artificial hybrids would be the most important. *R. amphibia* × *palustris* has clearly smaller sepals and petals, and also smaller petals in relation to the sepals. It has large, nearly clasping auricles, while in *R. amphibia* × *sylvestris* no or very inconspicuous auricles are seen. Finally the cauline leaves of *R. amphibia* × *palustris* are less deeply pinnatifid and have more rounded segments (Fig. 18, Plate VIII). These distinctions reflect some of the differences between *R. palustris* and *R. sylvestris*. There are some more characters of that type, e.g. pod-shape and serration of leaf-margins, whose value for evaluating unknown specimens is little, however, since *R. amphibia* might well account for about the same expression of these characters as *R. palustris*.

As far as F_1 hybrids on the tetraploid level are concerned there should consequently exist clear differences between the two actual combinations. The artificial pentaploid *R. amphibia* × *sylvestris* hybrids (J 188 × J 395) agree on the whole with the corresponding tetraploid but show, as could be expected, a closer resemblance to *R. sylvestris* (see Table V). Although only single samples out of the rich mass of biotypes have been employed in the experiments, any interpretation of the spontaneous hybrid populations should not be in contradiction to the facts on hybrid morphology obtained from crosses. Exposed to the mixed pollen environment in the experimental garden the *R. amphibia* × *palustris* plants set some well-developed seeds, none of which germinated, however. This does not exclude that other F_1s of this hybrid may be rather fertile. Both the tetra- and pentaploid *R. amphibia* × *sylvestris* plants set usually plenty of good seeds.

In Scandinavia and Britain the *R. amphibia* hybrids are only known from some rather well delimited areas, which cover only parts of the distribution range of *R. amphibia* itself. Each of these areas will here be treated separately, since the local situations are rather different and since the hybrids must have originated independently in each of them.

Hybridization at Lake Mälaren (Central Sweden)

The Mälar region, as taken here, comprises the whole lake as well as the affluents known to house hybrids (R. Fyris and R. Hågaån near Uppsala). *R. amphibia* hybrids have been found scattered all over this area, but are almost unknown elsewhere in Central Sweden (cf. App. 5). The area is the largest water system in N. W. Europe housing hybridizing *Rorippa* populations.

The populations of pure species. R. palustris is the most widespread of the three species, and is probably distributed in about equal frequency over the whole area. It does not form any dense populations, and often only a few individuals are present in a locality (cf. Ch. 4). The genotypic variation is inconspicuous. Open, and particularly muddy or sandy shores furnish the most favourable conditions.

R. amphibia is also distributed over the whole area without notable lacunes. It is found especially on shores with fresh and still open drift (cf. p. 21) where it may form dense populations, but often there are only a few or single flowering specimens in a locality. The species is on the whole morphologically uniform. The variation observed may be due to hybridization. Seed setting often fails, in most cases probably because of the self-incompatibility (cf. Ch. 4).

R. sylvestris is rare all over the area and, at least nowadays, absent from certain parts notably the northernmost inner bays, Ekoln–Ullevifjärdarna (see further below and Fig. 16). It is almost restricted to open, sandy-gravelly shores, which particularly exist where eskers cross the lake. Being still more sensitive than the other species to competition (cf. Ch. 6 B) it may have disappeared from many localities owing to the increased choking from reed vegetation. *R. sylvestris* is here more hemerophilous than the other two species, and in most localities inspected it seems dependent of clearances of the vegetation at landings, bridges etc. Only tetraploid *R. sylvestris* is known from L. Mälaren, but the morphological variation is still considerable. Some local forms can be distinguished. The possible origin of this variation by introgression will be discussed below.

Of these *R. palustris* is the only one able to have grown at the shores of the sea-gulf preceding L. Mälaren, as it sometimes does at the Baltic today. The other two are known only from freshwater and cannot have become established before the salinity had been considerably reduced. Suitable conditions may have prevailed from about the first millenium A.D. (cf. p. 101). The arrival of *R. amphibia* and *R. sylvestris* was discussed above, and to these events the starting-time for hybridization is of course connected.

Genesis of hybrids. More or less intermediate hybrid plants occur infrequently at L. Mälaren in restricted regions and mostly very locally. The known localities are mapped in Fig. 16. The following presentation aims at showing that only hybrids between *R. amphibia* and *R. sylvestris* are with certainty present at L. Mälaren. Doubtful specimens of course exist but I have not found evidence for the occurrence of *R. amphibia* × *palustris*.

With few exceptions (J 526) the Mälar hybrids in cultivation and sometimes in the field have nearly as good seed setting as the pure species. Seeds collected in nature often germinate to a high extent (70–80 %) and give rise to strictly euploid progeny of normal vigour. Cross-fertilization would here account for the seed-production. The great morphological variation of the progeny indicates high

Fig. 16. *R. sylvestris* and *R. amphibia* × *sylvestris*. Distribution on the shores of Lake Mälaren. Dots = herbarium records of *R. sylvestris*; circles = literature reports of *R. sylvestris*; triangles = herbarium records of *R. amphibia* × *sylvestris*; dots inscribed in triangles = herbarium records of both *R. sylvestris* and *R. amphibia* × *sylvestris*. The vertical lines denote localities from which chromosome numbers ($2n = 32$) have been verified. E = Bay of Ekoln; S = Stockholm; U = Bays of Ullevifjärdarna; UP = Uppsala; V = Västerås.

heterozygosity of at least one of the parent plants. This is in contrast to the uniformity of progeny raised from spontaneous *R. amphibia* seeds and of the F_1 generation of controlled interspecific crosses (see Ch. 5) and is also a proof of the hybrid nature of the actual plants.

The spontaneous Mälar material in cultivation does not include any plants approaching the artificial *R. amphibia* × *palustris* hybrids (cf. Table V). It is more difficult to find out if any progeny from back-crosses or from crosses between various hybrid derivatives exist. But most progeny from back-crosses to *R. amphibia* would cover a morphological variation range between *R. amphibia* and the F_1 hybrids. Unless very close to *R. amphibia*, the spontaneous hybrids in cultivation do not fall within this range as concerns important features, particularly the leaves, which are more deeply and narrowly pinnatifid than in the F_1 *R. amphibia* × *palustris* (see Figs. 18, 19).

Most back-crosses to *R. palustris* would give plants with deeply pinnatifid leaves but very small petals and prominent auricles. Small flowered clones exist

in fact in the cultivated material, e.g. J 526, which has totally barren ovaries and almost unfunctionable pollen. In J 1224 the petal-sizes are highly variable (Table V). Small flowers with narrow petals were also found in rather barren plants raised from seeds of certain *R. amphibia* × *sylvestris* clones interbreeding in nature. Such progeny displays a more random combination of parental characters but no features clearly pointing to the participation of *R. palustris* have appeared.

The small flowers of the Friesian *Nasturtium anceps* var. *micropetalum* (cf. p. 113 and Table V)[1] induced Borbás (1879*a*) to regard it as a *R. amphibia* × *palustris* hybrid, an opinion also held in Neuman (1901). A closer study of the plant reveals aberrancies in ovary shape and probably high female sterility. The small flowers are most certainly connected with that. I cannot find anything that excludes the possibility of *R. sylvestris* being the other parent—the foliage even seems very close to this species (Fig. 19 R). There are some more collections from R. Fyris of this or a very similar barren clone (1850 Th. Fries, UPS, 1857 Zetterstedt, UPS). If not combined with studies of fertility and of other characters small petals are thus no reliable indication of *R. palustris* as a component of a *R. amphibia* hybrid.

Small auricles may exist also in *R. sylvestris* hybrids, since they may occur in the parent species, but prominent to clasping ones would definitely point to *R. amphibia* × *palustris*. Such auricles have not been observed in the Mälar material.

As judged from the experimental crossing-products it seems highly improbable that F_1 clones of *R. amphibia* × *palustris* or any derivatives intermediate between F_1s and *R. palustris* would now exist at the lake. The autogamy and the absence of effective vegetative propagation in *R. palustris* would make back-crosses to this species rarer and the resulting progeny often less able to be established. Occasional participation of *R. palustris* in the hybrids can, on the other hand, of course not be totally excluded in clones very close to *R. amphibia* or with aberrant character combinations, but cannot be proved either. The material is clear derivatives of *R. amphibia* × *sylvestris* or ambiguous. In the following discussion only *R. amphibia* and *R. sylvestris* will thus be regarded as influencing the hybrid variability. Additional evidence from distributional facts in favour of this interpretation will be given later in this chapter.

Variability of hybrids. All hybrid clones investigated from L. Mälaren are tetraploid but they are morphologically highly divergent and seem to represent a series of intermediates between *R. amphibia* and *R. sylvestris*. This is shown in Fig. 17 for two characters clearly distinguishing *R. amphibia* from *R. sylvestris*, viz. pod-length and leaf-shape, the latter here expressed as length of the terminal seg-

[1] The Friesian collection called var. *micropetalum* is not uniform. E.g. on the sheet preserved in UPS one of the complete specimens is barren while the other seems to set seeds, has fairly good pollen and rather long petals.

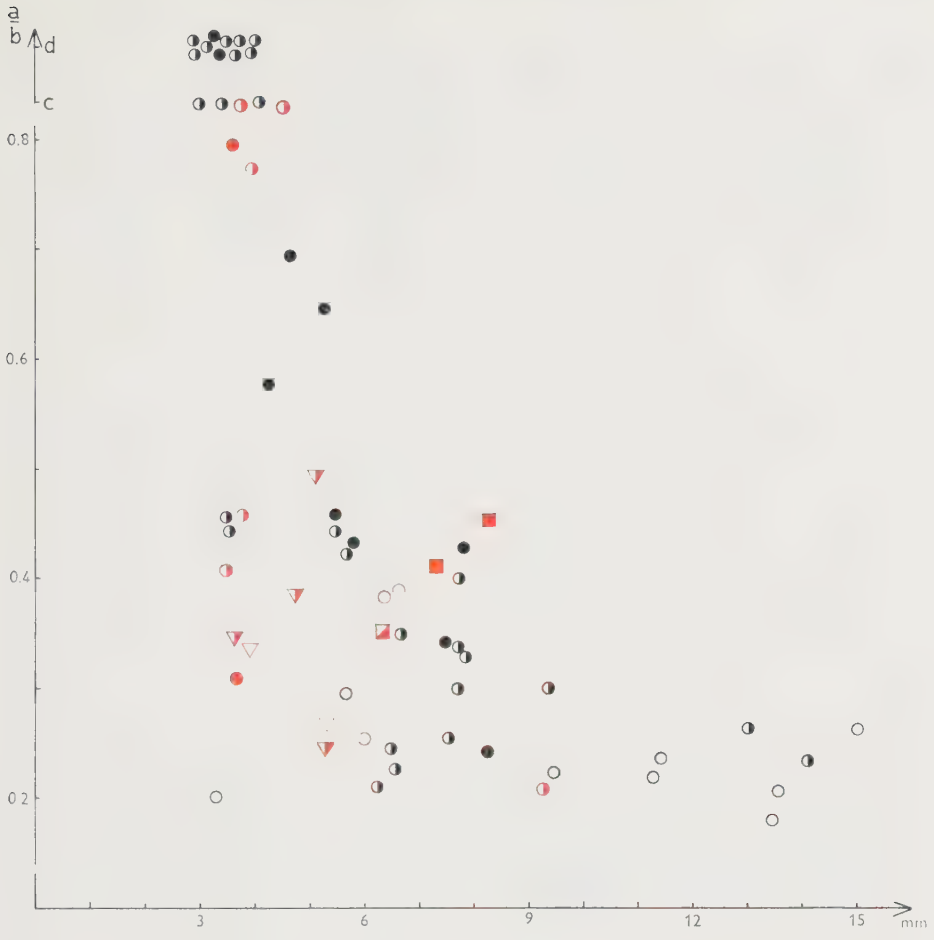

Fig. 17. Tetraploid *R. amphibia*, *R. sylvestris* and *R. amphibia* × *sylvestris*. Scatter diagram illustrating variation of *pod-length* (horizontal axis), ratio of *length of terminal leaf-segments* (a) to *total leaf-length* (b) (vertical axis) and *style-length*. Black symbols = spontaneous Mälar clones; red dots and circles = plants derived from spontaneous seeds of Mälar hybrids; red triangles = plants derived from back-crosses of Mälar hybrids to *R. amphibia*; red squares = plants derived from a cross between *R. sylvestris* (J 361) and *R. amphibia* (J 406). Filled symbols = styles longer than 1.5 mm; half-filled symbols = styles 1.2–1.5 mm; open symbols = styles shorter than 1.2 mm. The vertical axis is broken at 0.8; at "c" and "d" a/b = 1.0: "c" = deeply serrate cauline leaves; "d" = moderately serrate—dentate cauline leaves. Clones at "c" and "d" were classified as *R. amphibia*, those with pods longer than c. 9.3 mm as *R. sylvestris*, the rest as hybrids.

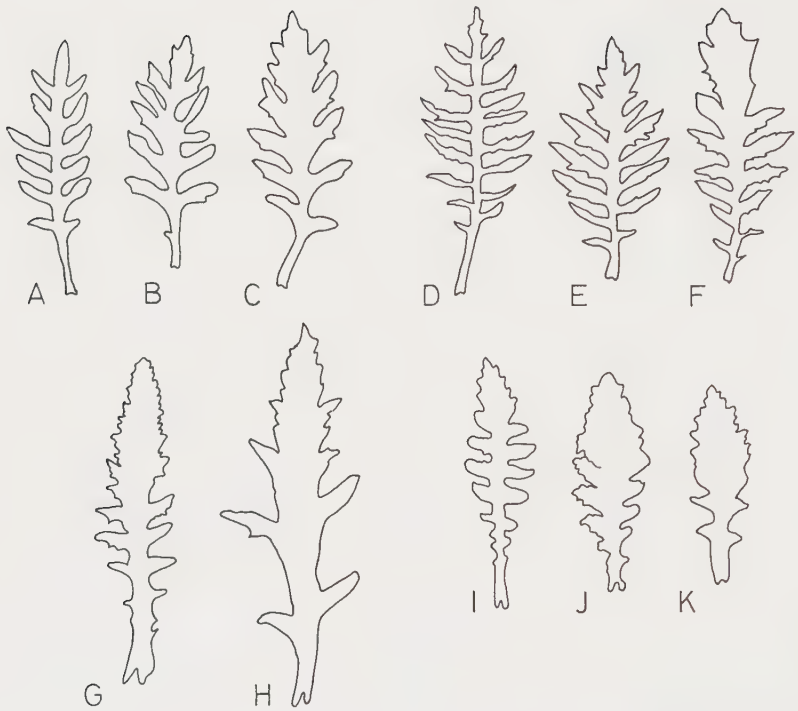

Fig. 18. Cauline leaves of artificial *Rorippa* hybrids. A–C: tetraploid *R. amphibia* × *sylvestris* (J 361 × J 406); series of leaves from near the base (A) to the middle of the stem (C). D–F: pentaploid *R. amphibia* × *sylvestris* (J 188 × J 395); series of leaves from near the base (D) to the middle of the stem (F). G–K: tetraploid *R. amphibia* × *palustris*. (G–H: J 379 × J 471, from specimen in flower (G) and in fruit (H). I–K: J 919 × J 950, series of leaves from near the base (I) to the middle part of the stem (K). All leaves except H from flowering specimens. ½ ×.

ments in relation to the length of the whole leaf. Cultivated material of *R. amphibia*, *R. sylvestris* and hybrids is plotted. Only highly fertile hybrids could of course be used for the diagram. The majority of the black symbols approximately form a curved zone, which means a markedly correlated variation between the characters illustrated. The variation in style-length displays on the whole the same picture. The longest styles are not, however, found in pure *R. amphibia* but in hybrids morphologically approaching this species. This phenomenon is met also in other regions and may be a heterosis effect, this much the more so as the actual plants are vigorous also in other respects. Also the variation in other characters, as size and shape of shoots, mode of growth and size of flowers is on the whole correlated in the same way (cf. Table V). This is the normal pattern where hybrid swarms are formed from two species, while biotypes with a more random combination of characters are rare (Anderson 1949). The few plants of the latter kind emanate

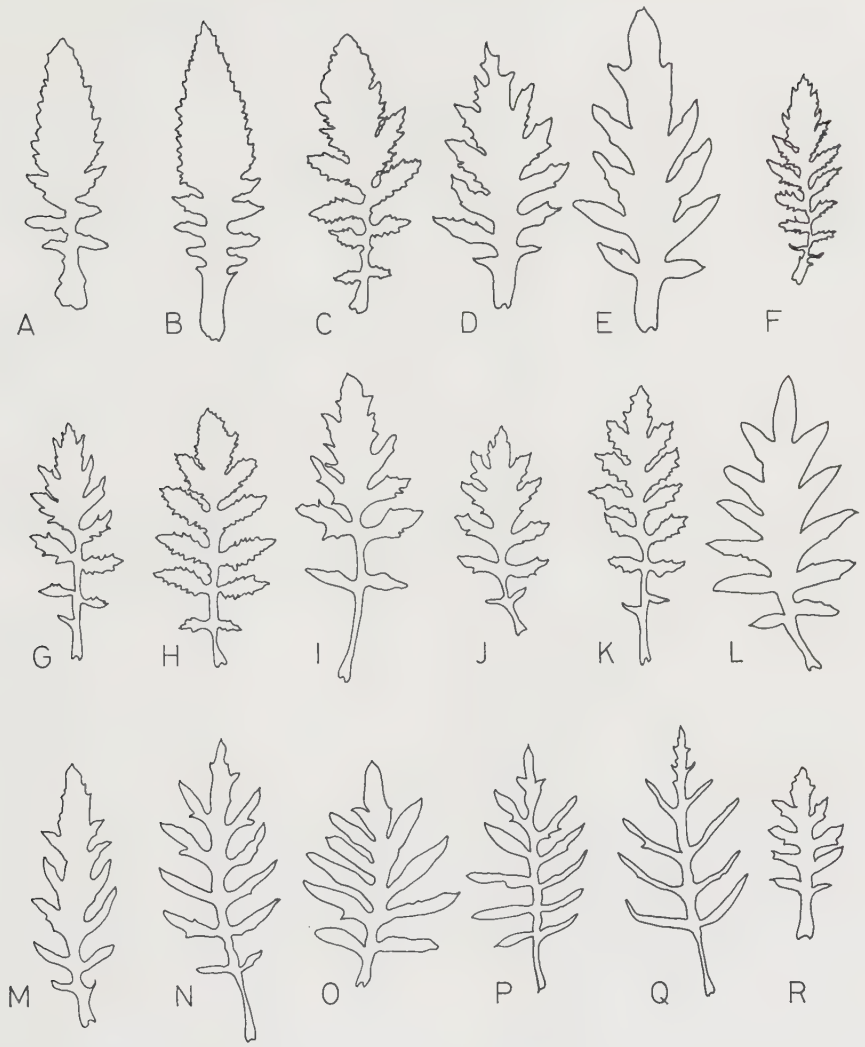

Fig. 19. Cauline leaves from the middle part of stems of *R. amphibia* × *sylvestris* from Lake Mälaren. A: J 344. B: J 924. C: J 385. D: J 526. E: J 339. F: J355. G: J 356. H: J 936. I: J 1222. J: J 920. K: J 921. L: J 1224. M: J 1251. N: J 347. O: J 371. P: J 387. Q: 1818 Wahlenberg, UPS. R: Fries, Herb. norm. No. XI. 36.

from hybrid swarms except J 1224 (see below and Table V). Hybridization between *R. amphibia* and *R. sylvestris* at L. Mälaren has led to an almost continuous variation from one parent to the other, evidently because back-crosses and segregations take place to each of the species to about the same degree, which does not mean, however, that the traces of hybridization are equally visible in both the parent

species. In many cases where species form fertile hybrids the following back-crosses are chiefly directed to one parent, and thus a more or less distinct gap appears in the morphological variation range to the other.

The diagram (Fig. 17) includes also progeny from crosses between Mälar plants[1] and from spontaneous seeds collected in Mälar hybrids. The F_1 progeny takes as expected an intermediate position. The hybrid progeny shows weaker character correlation than the spontaneous plants, which may indicate that it includes more unbalanced biotypes that have little chance of establishment in nature.

For a hybrid situation like that at L. Mälaren introgression would be suspected between the species engaged. Introgression would here mean variation in populations of one species in direction to the other species outside the spots where direct hybridization is taking place or where more or less intermediate biotypes are present. For *R. amphibia* that would mean that a wider variational range could be expected in the Mälar region than in e.g. the interior of Uppland, where *R. sylvestris* is absent. But no such difference was found which would imply that hybridization has not taken place on a scale sufficient to result in a real gene flow from *R. sylvestris* into the *R. amphibia* population. One reason for that is the short time, less than 2000 years (cf. p. 101), during which the species can have been in contact. Moreover *R. amphibia* is now and was most likely also earlier much more widespread than *R. sylvestris*, whose special ecological claims put a limit to its distribution. Hybridization can therefore only take place in very limited spots within the distribution range of *R. amphibia*. Hybrid biotypes dispersed independently have of course increased the number of hybridization spots. But a flow of genes that way into great parts of the *R. amphibia* population is made difficult by the prevailing vegetative dispersal of that species, which means an almost unlimited life-length of a single clone. One clone may predominate over a vast area, and crosses within a small part of its range would change the situation very little. Furthermore seedlings are not likely to be established within a *R. amphibia* population (see Ch. 4).

For *R. sylvestris* the situation is different. The sparse number of specimens seen (living as well as dried) are conspicuously unlike each other in many characters. The variation in *R. sylvestris* was discussed above, where also the special appearance of populations at central L. Mälaren was observed. Part of the variation seen can be interpreted as due to introgression, but the limited material available permits only cautious suggestions. In some clones, notably those with rounded leaf-segments, the styles are distinctly longer than in other Scandinavian *R. sylvestris* (c. 1.2 mm). Some other clones show the longest petals known in tetraploid *R. sylvestris* (cf. Fig. 10). These examples of variation point clearly

[1] Of the components of the cross J 361 (*R. sylvestris*) × J 406 (*R. amphibia*) the latter is not from L. Mälaren but from Finland (cf. App. 1).

towards *R. amphibia* and might be due to introgression. It is more difficult to explain the leaf-shape variation (cf. Fig. 12, F–H). The specimens from the westernmost part of the lake with deeply incised lateral segments (e.g. J 916, 1887 v. Porat) are especially remarkable. It seems improbable that repeated arrival of *R. sylvestris* clones accounts for all this variation. On the contrary isolated *R. sylvestris* clones within the much greater *R. amphibia* population would have excellent opportunities of producing hybrid seeds, which in the localities typical of *R. sylvestris* would have chances to establish new clones. Many of the *R. sylvestris* clones at L. Mälaren have only 10–20 % of fertile pollen grains, which may indicate interspecific hybridization to have occurred among the ancestors. The circumstances mentioned thus speak in favour of introgression as an important cause of the variation within *R. sylvestris* at L. Mälaren, although this cannot be proved by quantitative methods.

Distribution, ecology and dispersal of hybrids. The hybrids have very restricted occurrences, each rhizoclone covering some few m^2 or some tenths of meters along the shore, and often less. Also where more biotypes occur or where the single one present is divided into a number of rhizoclones the total area covered by hybrids is very small.

The longevity of the hybrids varies considerably. In shores kept free of competing vegetation they seem able to persist for long times, otherwise they may be highly ephemeral. The latter was verified on revisits to places where vigorous hybrids had grown two or three years earlier but could not be refound. Besides competition erosion by ice might be disastrous for an isolated hybrid population, which cannot be easily restocked from the surroundings. Although a hybrid rhizoclone may have considerable life-length, its special ecological claims and the difficulties to form larger clumps, would make each hybrid in the Mälar region susceptible to derangements and ephemeral. The Mälar hybrids are not so markedly hemerophilous as *R. sylvestris*, since they are often found at natural esker shores. Man's activity does not seem to have been a direct condition for the establishment of these *R. amphibia* × *sylvestris* hybrids, although it has in several cases certainly promoted them (e.g. J 526).

In most hybrid localities only one of the parent species was present. *R. amphibia* was often found at least in the vicinity, while *R. sylvestris* was seen together with hybrids in only one place (cf. J 186 and 921). In several cases herbarium specimens confirmed the earlier presence of *R. sylvestris* in places where today only hybrids were found (e.g. Skokloster, Svinnegarn, Strängnäs, Sundbyholm, cf. App. 4 and 5). In some localities a number of different hybrid biotypes are present (e.g. Sundbyholm) and sometimes these constitute a hybrid swarm growing within a very restricted area (Arnöhuvud, R. Hågaån at Lurbo, cf. App. 5). For some places herbarium specimens revealed the existence, at least previously, of still more

biotypes than those discovered in the field (e.g. Strängnäs). In places like those hybridization might have initiated and been followed by back-crosses leading to the segregation of various biotypes.

Isolated hybrid clones are rare at L. Mälaren. One example is the very *R. sylvestris*-like clones J 371 and J 372 from an esker close to Enköping. Most examples are available from the inner bays south of Uppsala, where hybrids are on the whole rather common (cf. above and Fig. 16), and occur isolated especially at points of eskers (J 355, 356, 1542). Richly seed-producing hybrid swarms, like the one at Arnöhuvud, may here act as centres for dispersal, perhaps by means of both seeds and vegetative parts. Isolated specimens with unusual character combinations, but in close agreement with plants raised from seeds collected from hybrid swarms, were found at some places at the bay of Ekoln, e.g. J 1224, which has probably originated within such a swarm. Vegetative dispersal must play a role at least secondarily in propagating a biotype into several rhizoclones. In this way a single clone seems to have become established and exclusive at the innermost part of the bay-system mentioned (Gorran-Ullevifjärdarna; J 355, 356, 936, cf. Table V).

A remarkable fact, concerning the whole inner bay-system (Ekoln–Ullevifjärdarna) is the absence of clones of pure *R. sylvestris*. It was not found during my own investigations of the area, nor are there any herbarium records. Some dots for *R. sylvestris* in Almquist (1929, Map 267) evidently stand for hybrids. The innermost certain occurrence at the lake itself of pure *R. sylvestris* is from Skokloster par., near the castle (1820, 1827 Wahlenberg, see App. 5). From later times only hybrids have been gathered there. This absence of *R. sylvestris* from a wide area where hybrids are rather frequent has been a chief argument for not considering the hybrids in particularly the northern part of Ekoln and in the lower Fyris valley as *R. amphibia* × *sylvestris*, but instead as *R. amphibia* × *palustris*, since the two latter species are both common in the bay system. As mentioned above E. Fries (1843) was the first to express a view in that direction. A couple of hybrid biotypes are so close to *R. sylvestris*, however, that the participation of this species is beyond doubt. One (J 1251) was found at Arnöhuvud in the hybrid swarm there (cf. above).[1] Several collections by Björkman (UPSV) from the northern and western shores of Skokloster parish also include biotypes very close to *R. sylvestris*. Another clone of this kind is J 387 (= 1939 Almquist UPSV), growing at the River Hågaån near its mouth into the northern part of the bay of Ekoln, a place where two more hybrid clones were discovered (J 385, 394). There are also two collections of *R. sylvestris* of Mälar-type (cf. p. 95) said to be from Uppsala at the river (1867 Thedenius, S. and 1873 Ahlberg, GB). The first is probably erroneous since Thedenius is not known to have collected in the area (Almquist 1965). The second may be correct, but the plant would have been ephemeral since it is otherwise unknown

[1] A probable indirect confirmation of the previous existence of *R. sylvestris* in this place offers a collection from Uppland: Skogstibble par., 1870 S. Almquist (UPS), where it was probably introduced with gravel taken from Arnöhuvud (see Almquist 1965, p. 158).

during the whole 18th and 19th centuries. In herb. Sommerfelt (O) there is one sheet labelled "*Sis. anceps*", which carries two specimens one of which is a *R. sylvestris*, the other a hybrid. These specimens were apparently collected at Uppsala by C. J. Hartman. The rich material from the R. Fyris collected south of Uppsala in the 19th century is richly fertile, and seems to comprise many biotypes. A number of these specimens show distinct traces of *R. sylvestris* morphology. Verification from living plants was not possible, since the Fyris hybrids have now completely disappeared, probably owing to choking vegetation (last collection from 1892, cf. App. 5).

The evidence that *R. sylvestris* is taking part in hybridization in the Uppsala region and the exclusion on morphological grounds of *R. amphibia* × *palustris* as growing there (cf. above), leaves two main alternatives open to explain the present situation at the inner bay-system. Either hybrid biotypes with genomes fairly close to *R. sylvestris* could have spread independently to the area and crossed with *R. amphibia* existing there. Or the species *R. sylvestris* itself was earlier growing in the area and has later disappeared, but initiated a biotype formation which is still going on. Similar but more local situations were referred to above for other parts of L. Mälaren, where *R. sylvestris* is no longer growing with the hybrid population. Even single clones of this self-incompatible plant in an environment of *R. amphibia* would during a few seasons produce a considerable amount of hybrid seeds. The rareness or final disappearance of one parent species, *R. sylvestris*, would imply that back-crosses were mainly carried out with the other species, *R. amphibia*, and perhaps ultimately lead to a widening of the variation pattern of that species. In the actual inner bay-system it is also easy to see a dominance of *R. amphibia* characters in the hybrid material. But the process would be slow since a single clone may have a practically infinite life-length. It cannot only survive but even contribute to the formation of new biotypes over a long period.

In the second case the clone or clones initiating hybridization are now extinct in the area, but otherwise there is no principal difference between the two alternatives, since both *R. sylvestris* and hybrids close to it are dispersed and form populations in much the same way. The comparative frequency of *R. sylvestris*, at least earlier, in the eastern part of L. Mälaren (cf. Fig. 16) all the way into Stockholm speaks in favour of dispersal of the species rather than of hybrids which at least today are very rare in that region. If *R. sylvestris* was earlier spread through shipping (cf. p. 101) it seems natural to imagine the species to have been established at least temporarily also along the northern part of the trade-way to Uppsala, viz. Ekoln and the Fyris valley below the city.

Hybridization in Skåne (S. Sweden)

Nasturtium anceps was first reported from Skåne by Wahlenberg 1824 (see above) and in the 19th century floras of the province (Fries 1835, Lilja 1870, Areschoug 1881) from streams in the western, southern and north-eastern parts.

Neuman (1901) discerned both *R. amphibia* × *palustris* and *R. amphibia* × *sylvestris* as present in this province, and so did Weimarck (1963). Morphological studies of the Skåne hybrids give, however, no more room for the existence of *R. amphibia* × *palustris* hybrids than was the case in the Mälar region (cf. Table V and below).

The most striking feature of the *Rorippa amphibia* hybrids in Skåne compared with those at L. Mälaren is the existence of pentaploid clones as well as tetraploid ones. Pentaploid *Rorippa* hybrids are not known from any other Nordic area, but there is one find from Britain (J 1148). I found pentaploids in only four localities, viz. in Kristianstad (N. E. Skåne), near Malmö, at the stream Fränningeån and at L. Vombsjön (all three in S. Skåne). There are morphological dissimilarities between them (Table V) and they have probably arisen independently of each other. The origin from crosses between *R. amphibia* and *R. sylvestris* seems clear in all cases and the chromosome number gives additional support to that view. The last-mentioned occurrence is the most important and will be treated in some detail.

The shallow lake Vombsjön (now not over 9 m deep; area 12.5 km^2) lies in a region of sand and has today along the eastern, northern and western sides open, sandy and rather exposed shores. They are partly bordered by a rather dense helophyte vegetation, where *R. amphibia* is an important constituent. Rather frequent in moist sand is also *R. palustris*. Higher up on the open sand hexaploid *R. sylvestris* (J 1235, 1307; both probably the same clone) was found on the eastern side, and herbarium specimens of similar appearance exist from other places at or near the lake (1943 Linders, LD).

Pentaploid hybrids were found both at the eastern and western sides of the lake in open sandy parts of the shore, above the helophyte belt. They propagate by vigorous root runners. Their general appearance is exemplified in Plate VII, leaf-shape in Fig. 20 G. The morphological variation in the cultivated Vombsjö hybrids is moderate (cf. Table V). It concerns e.g. style-length, auricles, pubescence and leaf-shape, but all have the same general habit. Both in nature and in cultivation the seed-production is rich. The pods generally ripen to a definite length. The ovaries seem here to function better than the pollen, whose quality is very low throughout (Table V). Spontaneous seeds germinated in high frequency. The morphology of the plants is very close to the artificially produced pentaploid *R. amphibia* × *sylvestris* hybrids (cf. Table V), which also in general show good seed setting.

Progeny from spontaneous seeds of the Vombsjö pentaploids was aneuploid throughout ($2n = 33$–38). In spite of that only euploid plants were found at the lake. This indicates that all the hybrids growing there are F_1s from crosses between the tetraploid *R. amphibia* and the hexaploid *R. sylvestris*, and that aneuploids have very small chances of becoming established in a natural environment. The

small variation between the spontaneous pentaploids contrasts sharply with the aneuploid progeny, which is highly variable in several morphological features. Part of these aneuploids are vegetatively very vigorous, and their fertility is very variable. The seeds formed in the pentaploids are most certainly the result of outbreeding, since the pentaploid hybrids are strongly self-incompatible—whether due to inherent factors like the parent species or simply to the bad pollen quality has not been settled. The chromosome numbers indicate back-crosses to *R. amphibia* in the cases examined. The slight morphological differences which all the same exist between the pentaploids when kept in cultivation, make probable that there are several clones produced from crosses between *R. amphibia* and *R. sylvestris*. The observation of small chromosomal fragments in mitotic metaphase plates in some pentaploids points in the same direction.

The age of the hybridization at L.Vombsjön cannot be established with certainty. There are, however, no herbarium specimens collected before the 1940-ies (earliest 1946 Linders, LD). Perhaps the regulation of the lake in the 1940-ies, which implied a decrease in water volume so considerable that the greatest depth diminished from 15.5 to 9 m and the exposure of a large area of the bottom, which became new shores (Linders 1946, Mathiasson 1958) favoured the establishment of the hybrids. Probably the hexaploid *R. sylvestris* is a recent neophyte at the lake. It is not in morphological agreement with the clones of *R. sylvestris* known from Skåne in the 19th century (cf. Ch. 6 B). This species would have found good conditions on the new sandy shores and any hybrids produced with the *R. amphibia* population earlier existing at the lake would have found good possibilities to spread. Two older collections of *R. sylvestris* at L. Vombsjön (1900 and 1910, cf. App. 4) do not coincide with the hexaploid but with other clones from Skåne of that time. They may be parents of the tetraploid *R. amphibia* × *sylvestris* hybrids, also known from L. Vombsjön.

At R. Fränningeån a single pentaploid rhizoclone (J 1312) was growing on a sandy shore together with a tetraploid hybrid (J 1314).

The remaining two occurrences of pentaploid hybrids in Skåne were found at places directly created by man, and in both only single plants were discovered. One of these was the slope of a ditch near the city of Malmö (J 534), where no other *Rorippa* was seen in the vicinity. On a visit there two years after the discovery the hybrid was not refound. J 534 is very similar to the above-mentioned J 1312 (cf. Table V). These clones agree more with pure *R. sylvestris* than the other pentaploids from Skåne. The other was at a canal in the town of Kristianstad (J 1085). It has in contrast to the Vombsjö pentaploids good fertility (cf. Table V). In herbarium material from this town, especially from the 1920-ies and 1930-ies, to a large extent collected by P. Tufvesson, a very rich amount of *Rorippa* biotypes seems to be represented, both of *R. sylvestris* and of its hybrids (see further in App. 4, 5 and 7). Repeated introductions as well as hybridizations

Fig. 20. Cauline leaves from the middle part of stems of spontaneous *Rorippa* hybrids. A–E: tetraploid Scandinavian *R. amphibia* × *sylvestris* (A: J 520. B: J 532. C: J 535. D: J 1095. E: J 1314). F–K: pentaploid Swedish *R. amphibia* × *sylvestris* (F: J 536. G: J 1091. H: J 1311. I: J 534. J: J 1312. K: J 1085). L–Q: tetraploid British *R. amphibia* × *sylvestris* (L: J 1169. M: J 1168. N: J 1150. O: J 1170. P: J 1172. Q: J 1171). R: pentaploid British *R. amphibia* × *sylvestris* (J 1148). S–T: *R. amphibia* × *palustris*. (S: tetraploid, J 1167. T: triploid, 1946 Howard, UPS). U: *R. palustris* × *sylvestris* (Samuels.: Pl. Suec. exs. No. 908).

between the meeting clones would have occurred. Not much was refound of this flora on visits in the 1960-ies, but plants at hexa-, penta- and tetraploid levels were collected, in the last case only *R. amphibia*, however.

Tetraploid *R. amphibia* hybrids were found at a few lakes and rivers among those L. Vombsjön, but not close to the pentaploids. Some of them are listed in Table V, and they seem all to fall within the series *R. amphibia* × *sylvestris*. But the tetraploid Skåne hybrids are partly rather unlike those of L. Mälaren, especially some very tall and vigorous clones with very long styles and large pods (J 532, 1095). This might be a heterosis phenomenon. Similar giant pods are actually sometimes met with in *R. amphibia* in Skåne (e.g. J 1096). Herbarium specimens of hybrids closely matching these tetraploids exist from some further water systems in the south-western part and from the river Helgeå near Kristianstad (cf. App. 5). *R. amphibia* hybrids are in Skåne almost confined to the regions where *R. sylvestris* is known as a shore plant, a matter that further supports the view that these hybrids were derived from crosses between this species and *R. amphibia*.

Hybridization in the rest of Scandinavia

Outside the regions treated above *R. amphibia* hybrids are extremely rare in Scandinavia. From Denmark only a few herbarium specimens were found, which are likely to be *R. amphibia* × *sylvestris*, viz. from Jutland (Hvideå in Thy and Ribe, in the latter place sought in vain in 1966), Sjælland (Tjæreby near Korsör) and Bornholm (Nexö), cf. App. 5. These were all cited by Pedersen (1958) as *R. amphibia* × *sylvestris*, but the rest of the collections listed by him as this hybrid are apparently the hybrid *R. austriaca* × *sylvestris* (see below and App. 5 and 7). In all localities the hybrid might have arisen locally, though this is doubtful for the Thy find. From Ribe and Korsör there are also finds of almost pure *R. sylvestris* (cf. App. 4). From Bornholm both *R. sylvestris* (cf. App. 4) and *R. amphibia* have been reported (Bergstedt 1883, A. Larsen 1956) but I have not found any voucher specimens of the latter. Although *R. amphibia* hybrids are by no means frequent in Skåne, they are remarkably more rare in Denmark. But in that country *R. sylvestris* has not been known to have had a foothold in many water systems where *R. amphibia* is common. Immediately south of Denmark, in Schleswig-Holstein, a great number of hybrid finds, not checked by me, have been made (Christiansen 1953).

From the rest of Scandinavia only a few certain finds of *R. amphibia* hybrids are known. One was discovered in 1959 in Finland, Ostrobottnia borealis, at a branch of the Torne River near its mouth and close to the Swedish frontier. The circumstances on this find were treated in detail by Hylander (1961). Since it was growing in the vicinity of both *R. amphibia* (cf. p. 111) and *R. palustris*, it was natural to interpret the hybrid as formed by these two species. In 1961 I collected material

of this plant for cultivation. I found it to be tetraploid, but it showed hardly any of the features characterizing the artificial F_1 hybrids *R. amphibia* × *palustris* (cf. Table V, Fig. 20 A). If it had been produced this way and on this very locality the single hybrid clone found should reasonably be a F_1 progeny. The actual hybrid has large flowers, no auricles, nearly petiolate cauline leaves and a leaf-shape on the whole close to artificial *R. amphibia* × *sylvestris*. In my opinion this hybrid must rather belong to the series *R. amphibia* × *sylvestris* and consequently it cannot have originated on the spot, since *R. sylvestris* is unknown in the region (cf. Fig. 13).

Long distance dispersal must account for the occurrence of *R. amphibia* in the same place (cf. p. 111). But it does not seem improbable that the species and its hybrid have been dispersed together as seeds from a region where hybridizing populations are frequent. A small sample of seeds from such a place may contain seeds of very different genotypes. Some place in Central Europe would be a possible place of origin, rather than any of the Swedish occurrences which are not situated along communication routes, those at L. Mälaren possibly excepted. But the Torne River hybrid is not similar to any clones known from the Mälar region. Anthropochorous seed-dispersal might have occurred in this case, although this seems to be unusual for *R. amphibia* and its hybrids in comparison with e.g. *R. austriaca* × *sylvestris*. A reason for that is perhaps that the *R. amphibia* hybrids, like *R. amphibia* itself, can only be established in moist localities and are therefore without possibility in many places where *R. austriaca* hybrids grow (cf. below). Moreover the habitats make their dispersal with cereals etc. less probable. But the special situation at the Torne River, where a road-bank and a bridge cross a river arm with flat shores would be favourable for the establishment of seedlings. Bird dispersal can of course also be imagined.

There are also two isolated Swedish collections of *R. amphibia* × *sylvestris*, probably correctly labelled, one from Östergötland at Vreta Kloster (1888 Redelius, S), the other from Närke, Örebro, Ekebäck (1898 Bågenholm, LD). From the first region both parent species are known, to the second place the hybrid might have been taken from L. Mälaren through shipping. From Hälsingland (Sweden) and Hordaland (Norway) specimens exist that are not possible to determine with certainty (cf. App. 5).

In many Scandinavian floras from the 19th century reports of *Nasturtium anceps* from still more regions are found. They seem all to be mistakes, in general for divergent clones of *R. sylvestris*.

From what has been said above it is evident that besides some cases of probable long-distance dispersal no *R. amphibia* hybrids were discovered—neither in the field nor in herbaria—outside regions where both *R. amphibia* and *R. sylvestris* are distributed. Important areas exist where *R. amphibia* and *R. palustris* alone are sympatric, notably the Kumo River and parts of its lake system in Finland,

central and northern Uppland and large parts of Skåne in Sweden, as well as large parts of Denmark. The two species were observed together or close to each other in many places. The absence of hybrids in these areas confirms the assumption that *R. amphibia* × *palustris*, in contrast to *R. amphibia* × *sylvestris*, is a hybrid combination very rarely realized in nature.

Hybridization in the British Isles

It was not possible to make a detailed analysis of the British *R. amphibia* hybrids, since only a very limited material was kept in cultivation. Determinations of the herbarium material were based upon experience from the Nordic hybrid populations and upon studies of the distribution and variation in the British Isles of the putative parent species. Such methods could be used for Britain, where the material is limited and the situation rather simple, but not for Continental Europe with its overwhelming material (cf. below). The hybrid finds reported in the following are to be taken only as examples. I do not attempt a complete account of the British hybrid collections studied and only fairly clear specimens are therefore cited.

From the British Isles both *R. amphibia* × *palustris* and *R. amphibia* × *sylvestris* have been reported (cf. Dandy 1958, Clapham, Tutin & Warburg 1962). As concerns the former hybrid both works refer to the rather well-known plant from the Thames near Kew, which was first reported by Britton (1909) and later turned out to be a triploid (Howard 1947*c*, cf. Ch. 2). It certainly derives from a cross between diploid *R. amphibia* and tetraploid *R. palustris* occurring at the same river (Howard op. cit.), where it has spread vegetatively. The Thames hybrid shows considerable agreement with the artificial, tetraploid *R. amphibia* × *palustris* e.g. in habit, pod-shape and flowersize, but resembles *R. palustris* particularly in leaf-shape (Table V, Fig. 20 T). The triploid seems to be completely barren with empty pollen grains and no seed setting. Unfortunately I have not had this triploid in cultivation and the statements are based upon the numerous dried specimens preserved (K, BM).

In Gloucestershire, Tewkesbury a tetraploid clone (J 1167) was found, which for morphological reasons most certainly represents a *R. amphibia* × *palustris* hybrid (cf. Table V and Fig. 20 S). It is very vigorous in cultivation and also its habit reminds greatly of the artificial *R. amphibia* × *palustris* hybrids but shows much better fertility than those. It was growing in a ditch close to a road-bank and not far from the R. Avon, along which, however, only other hybrids were seen (cf. below).

British records of *R. amphibia* × *sylvestris* are sparse both in herbaria and in literature, but field studies and perusal of herbaria revealed that this hybrid is not rare at a number of lakes and rivers. I collected it from the Severn and its tributary R. Avon in Gloucestershire and Worcestershire (J 1168, 1169, 1170, 1171, 1172),

where all plants were tetraploid, and at the R. Arun in Sussex, where both a tetraploid (J 1150) and a pentaploid hybrid (J 1148) occurred (for morphological data see Table V and Fig. 20). A hybrid from R. Ouse in Cambridgeshire (at Earith) was found to be tetraploid by Howard (unpubl., voucher specimen in UPS). Evidently both tetraploid and hexaploid *R. sylvestris* take part in hybridization with tetraploid *R. amphibia*, which latter cytotype is the only one found in water systems housing *R. amphibia* × *sylvestris* hybrids.[1] From the Thames valley, where *R. amphibia* is only known as diploid, I have seen herbarium specimens most probably being *R. amphibia* × *sylvestris* only from the vicinity of Oxford (e.g. 1857 ex herb. Boswell, OXF). Along other rivers extensive hybridization has taken place. From a number of these rivers repeated collections of intermediate hybrid specimens exist. One or both of the supposed parents are often represented. Examples are available from R. Mole in Surrey (NMW 28 · 131 · 378), R. Arun in Sussex (Herb. Borrer K, J 1148, 1150), R. Ouse in Yorkshire (1865 Baker, CGE).

In still more cases there is evidence of extensive hybridization, leading to distinct signs of introgression in *R. sylvestris*, pure specimens of which were in some cases not found at all. One example is R. Severn, where hybrids occur at least from Shrewsbury down to Tewkesbury (1837 Babington CGE, Bloxam CGE, 1903 Brickham CGE, 1884 Linton BM, 1844 Westcombe BM, CGE, 1953 Sandwith K, J 1168–72). J 1171 and J 1172 are morphologically and ecologically very close to *R. sylvestris*, but show distinct *R. amphibia* features, J 1171 in leaf-shape and pod-width, J 1172 in plant height and style-length (Table V, Fig. 20, P–Q). They are classified as hybrids since the influence of *R. amphibia* seems beyond doubt. I have not seen any pure *R. sylvestris* from R. Severn neither in the field nor in herbaria. Along R. Wye (Monmouth and Herefordshire) where intermediate hybrids are also present (NMW 24 · 503 · 2, 1891 Armitage BM, 1916 Long BM, 1904 Riddlesdell BM, 1949 Townsend K), all collections labelled *R. sylvestris* carry signs of *R. amphibia*, particularly in the lengths of the styles (1.5–1.7 mm) of the partially fertile pods (NMW 28 · 131 · 376, 30 · 431 · 1, 35 · 574 · 3, 37 · 524 · 3, 39 · 505 · 2). From a tributary to R. Wye, R. Usk, a collection of *R. sylvestris* exists, which falls quite within the normal variation range of the species (NMW 41 · 237 · 10). Other water systems from which extensive hybridization is documented are R. Avon with affluents in Somerset-Gloucestershire (1920 Davis K, 1860 Grindon CGE, 1882 Murray BM, 1916 Marshall BM, 1884 Painter BM) and R. Ouse with its tributary R. Cam in Cambridgeshire–Huntingdonshire (Sell & Walters No. 54/209 CGE, 1951 Walters CGE, 1844 Newbould CGE, 1925 Druce OXF, cf. above).

In Ireland *R. amphibia* × *sylvestris* was reported from Co. Leitrim by Praeger

[1] From the Severn system no pure *R. amphibia* was examined but the hybrid J 1169 is morphologically very close to that species and most certainly a back-cross product on the tetraploid level.

(1909), and recent collections of *R. sylvestris* with morphological traces of *R. amphibia* exist from L. Allen in Leitrim-Roscommon (1962 Booth, CGE). *R. sylvestris* collections of similar appearance are present from L. Inchiquin in Co. Clare (1948 Dony K, 1905 Praeger BM). More intermediate specimens were seen from a river at Ennis in the same county (1958 Goodana & Dony BM), from Co. Waterford, Cappoquin (Sandwith No. 3991 K, NMW) and from L. Erne in Co. Fermanagh (1945 Meikle, K, Meikle Nos. 116, 2123, K). It can be questioned whether the curious leaf-shape typical of Irish *R. amphibia* (Fig. 15, H–I) is not a character intrograded from *R. sylvestris*.

Conclusions and comparisons with Central Europe

From the above account it is evident that hybrids between *R. amphibia* and *R. sylvestris* are often produced where the species grow together, at least where *R. amphibia* is represented by a tetraploid population. It is also clear that hybrid derivatives may spread independently, but apart from exceptional cases (cf. p. 130), only within the boundaries of a water system. Unlike *R. austriaca* × *sylvestris* (see below) and in spite of their hemerophily they have not been successful as weeds. The same seems to be true for Central Europe, where rich collections of *R. amphibia* hybrids exist from e.g. France, Switzerland, the Netherlands, Germany and further eastwards. They are mostly from larger river systems, but there are occurrences outside those (cf. Hegi 1958–63). The population in part of L. Bodensee (in the Rhine system) was thoroughly discussed by Baumann (1911), who employed for it the name *Nasturtium anceps* (Wg) Rchb. Referring to the absence of one of the possible parent species (*R. sylvestris*) at the shores studied and to the completely different ecological behaviour he believed to characterize *R. sylvestris* in comparison with "*N. anceps*", Baumann emphatically rejected any hybrid theory for the latter, but declared it to be a non-hybrid intermediary (cf. p. 112) between *N. amphibium* and *N. sylvestre*. This opinion was also held by Schinz & Thellung, who in 1913 launched the name *Rorippa prostrata* (Bergeret) Sch. & Thell. for this taxon (cf. Ch. 7). After that *R. prostrata* has been taken up as a species in many Central European floras (e.g. Hegi 1958–63, Rothmaler 1963, Heukels & v. Ooststroom 1956), although often with a reservation for its hybrid nature.

The observations from Nordic and British hybrid populations may not be applied to the situation in Central Europe. But at the present stage of knowledge it seems probable that these intermediate plants have originated in Central Europe within each water system separately as they certainly did in Scandinavia. Parallel populations, morphologically agreeing, will consequently exist, whose genetical relationship is indirect via the parent species. Where pentaploids have originated stronger barriers to back-crossing operate, which may result in a discontinuous variation towards the parents, if, like at L. Vombsjön, aneuploids are not established. In any case *Rorippa prostrata* will be a polyphyletic taxon, morphologically

Table V. Data

The measures given are mean values and/or extremes. Where the range
All spontaneous samples

Collection	Percentage good pollen[a]	Petal length (mm)	Sepal length (mm)	Style length (mm)
R. amphibia × *palustris*				
1946 Howard (UPS), $2n = 24$	0	2.2–2.5	2.0–2.2	0.7–0.8
J 1167, $2n = 32$	85	3.4 (3.1–4.0)	2.1 (1.9–2.5)	1.4 (1.2–1.5)
F_1 of J 379 × J 471, $2n = 32$	15	2.6–3.2	1.8–2.2	1.1–1.4
F_1 of J 919 × J 950, $2n = 32$	3	2.6–3.0	1.8 (1.5–2.1)	1.0–1.4
R. amphibia × *sylvestris* ($2n = 32$)				
Mälar hybrids				
J 339	50	4.0–4.3	2.2–2.5	1.5 (1.4–1.6)
J 344	65	4.3–4.6	2.4–2.6	1.8 (1.5–2.0)
J 347	50	4.0 (3.7–4.1)	2.2 (2.0–2.3)	1.3 (1.2–1.4)
J 355	70	3.6 (3.4–4.0)	2.2 (2.0–2.5)	1.3 (1.2–1.5)
J 356	75	3.7 (3.3–4.0)	2.3 (2.2–2.5)	1.4 (1.2–1.5)
J 371	80	4.3 (4.0–4.6)	2.5 (2.3–2.6)	1.3 (1.2–1.5)
J 385	45	3.5 (3.3–3.7)	2.2 (2.1–2.4)	1.3 (1.1–1.5)
J 387	50	3.8 (3.5–4.1)	2.3 (2.2–2.5)	1.3 (1.0–1.4)
J 526	10	3.0 (2.8–3.1)	2.0 (1.7–2.4)	—
J 920	90	4.1 (3.8–4.2)	2.2 (2.0–2.5)	1.3 (1.2–1.5)
J 921	80	4.0 (4.0–4.3)	2.5 (2.3–2.7)	1.5 (1.3–1.8)
J 924	70	4.2 (3.9–4.5)	2.2 (2.1–2.3)	1.8 (1.5–1.9)
J 1222	60	4.3 (3.9–4.7)	2.6 (2.3–2.7)	1.2 (1.1–1.3)
J 1224	50	2.2–4.7	1.6–2.4	1.1 (0.9–1.2)
J 1251	15	3.8 (3.6–3.9)	2.0–2.2	1.5 (1.5–1.6)
1818 Wahlenberg (UPS)[f]	35	3.5–4.0	2.2–2.4	—
Fries' Herb. norm. XI. 36[f]	0	c. 1.5	1.5–1.7	—
Skåne hybrids				
J 532	35	4.2–4.4	2.5–2.8	2.6 (2.1–3.1)
J 535	—	—	—	1.6 (1.4–1.9)
J 1095	—	—	—	1.6 (1.5–1.8)
J 1314	90	4.9 (4.1–5.5)	3.0 (2.8–3.5)	1.2 (1.0–1.4)
Finnish hybrid				
J 520	80	4.7 (4.3–5.5)	3.2 (3.0–3.6)	2.3 (2.1–2.5)
British hybrids				
J 1150	90	3.7 (3.3–4.4)	2.6 (2.4–3.0)	1.4 (1.2–1.6)
J 1168	65	3.9 (3.7–4.0)	2.5 (2.4–2.6)	1.1 (1.0–1.3)
J 1169	80	5.0	2.8	1.2 (1.2–1.5)
J 1170	35	3.8–3.9	2.5	1.2–1.5
J 1171	55	4.2–4.5	2.0–2.3	0.9 (0.8–1.0)
J 1172	30	3.8–4.3	2.2–2.3	1.2
F_1 of J 361 × J 406	70–95	4.1 (3.9–4.6)	2.4 (2.3–2.6)	1.6 (1.1–2.3)

about hybrids.

of mean values from various plants is given the figures are in italics.
were measured in cultivation.

Length of ripe pods (mm)	Pod shape[b]	Auricles[c]	Pubescence[d]	Plant height (cm)	Mode of growth[e]	Foliage see Fig.:
—	c. 2	4	0	c. 100	E	20 T
5.2 (4.7–5.6)	2.9	4	2	62–74	D–A	20 S
3.8–4.2	2.1	4	0	62	A	18 G–H
3.5–4.0	c. 2	4	0	50–68	A	18 I–K
7.5 (6.2–9.8)	5.6	2	3	52–60	D–A	19 E
4.6 (4.3–5.3)	2.2	1	0	53	E	19 A
7.7 (7.3–8.5)	5.6	2	3	35–40	A–E	19 N
7.6 (7.1–8.5)	4.4	2	3	35–46	A–E	19 F
7.8 (7.4–8.4)	4.4	2	3	35–47	E	19 G
9.3 (9.0–10.0)	6.4	1	0	28–38	E	19 O
5.7 (5.2–6.2)	3.6	1	3	41–52	E	19 C
6.2 (5.5–7.0)	4.3	1	0	40–58	A	19 P
—	—	0	0	47–61	E	19 D
7.5 (7.0–7.9)	5.2	1	0	52–56	A–E	19 J
8.2 (7.6–9.0)	5.4	2	2	48–54	A–E	19 K
5.4 (5.0–5.8)	2.8	2	2	52–60	E	19 B
6.5 (6.1–7.0)	5.4	2	3	42–48	E	19 I
3.3 (3.0–4.0)	1.8	2	0	55–68	A–E	19 L
7.8 (7.2–8.2)	5.7	1	0	35–38	A	19 M
—	—	1	0	>55	A	19 Q
—	—	1	0?	>30	A	19 R
8.0 (7.2–8.3)	3.7	2	1	–90	A	20 B
5.4 (5.1–6.1)	2.6	0–2	0–1	–77	A	20 C
9.3 (8.6–10.8)	6.0	1	0	65	A	20 D
7.4 (6.6–8.2)	4.2	0	0	60–63	A	20 E
6.4 (6.0–7.0)	4.0	0	0	58	E	20 A
8.6 (8.1–9.4)	4.5	1	2	67–68	A	20 N
8.9 (8.5–9.2)	5.4	1	2	51–63	A	20 M
6.3 (6.0–7.1)	3.4	2	3	72–79	E	20 L
6.0–6.2	4.4	1	3	30–34	A	20 O
7.9 (7.5–8.4)	5.4	1	2	29–35	D–A	20 Q
9.5–11.5	7.2	1	1	45–47	E	20 P
7.5 (6.6–8.6)	4.9	0	2	39–60	D–A	18 A–C

Collection	Percentage good pollen[a]	Petal length (mm)	Sepal length (mm)	Style length (mm)
R. amphibia × *sylvestris* (*2n* = *40*)				
J 534	5	3.5–4.2	2.2–2.4	1.0–1.2
J 536	20	4.3 (4.1–4.5)	2.8 (2.7–3.0)	1.7 (1.3–2.2)
J 1085	70	4.1 (3.7–4.6)	2.4 (2.2–2.6)	1.3 (1.1–1.5)
J 1091, 1237, 1311	0–2	*3.6–4.2*	*2.1–2.3*	*1.2–1.6*
J 1148	40	3.0 (2.7–3.2)	2.7 (2.5–2.8)	—
J 1312	0	—	—	0.9 (0.8–1.0)
F_1 of J 188 × J 395	60–85	*3.3–4.5*	*2.2–3.2*	*0.9–1.4*
R. austriaca × *sylvestris* (*2n* = *32*)				
J 540	80	3.5 (3.4–3.7)	2.2 (1.9–2.5)	1.3 (1.2–1.4)
J 541	85	3.5 (3.3–3.8)	2.2 (2.0–2.3)	1.3 (1.2–1.5)
J 856	15	3.5 (3.2–3.9)	2.2–2.4	0.8 (0.7–0.9)
J 868	< 1	3.9 (3.8–4.1)	2.3 (2.0–2.5)	1.2 (1.0–1.3)
J 872	25	3.5–3.9	2.3–2.6	1.3 (1.2–1.4)
J 1090	75	4.1 (3.9–4.3)	2.6 (2.5–2.9)	1.3 (1.1–1.4)
J 1220	80	3.4 (3.2–3.5)	2.4 (2.1–2.5)	1.3 (1.2–1.5)
?(cf.p. 138) J 1114	40	4.1 (3.9–4.5)	2.4 (2.3–2.6)	1.0 (0.9–1.0)
R. palustris × *sylvestris*				
Pl. Suec. exs. No. 908	15	2.7–3.2	1.8–2.2	0.9–1.1

[a] Values above 5 % are approximated to every 5 %.

[b] Pod-shape is length/width of ripe pods.

[c] 0 = no auricles; 1 = small auricles at some leaves; 2 = small auricles at most or all leaves; 3 = prominent auricles; 4 = nearly clasping auricles.

variable and indistinctly delimited from *R. amphibia* and *R. sylvestris*. It could hardly anywhere be true breeding. It does not seem justifiable to maintain a taxon of this kind.

The *Rorippa palustris* × *sylvestris* hybrids

Reports of the hybrid *R. palustris* × *sylvestris* (often under the name *R. islandica* × *sylvestris*) are frequent for wide areas of North and Central Europe (cf. Hegi 1958–63). Nowadays one of the species erected by Tausch (1840), *Nasturtium barbaraeoides* is usually identified with the actual hybrid, but that was not the opinion of earlier authors (Čelakovský 1874, Borbás 1879*a*) and does not seem justifiable to judge from Tausch's own description (cf. Ch. 7). It is evident that both in N. W. Europe and elsewhere many collections have erroneously been attributed to this hybrid. As a rule diverging *R. sylvestris* specimens have been

Length of ripe pods (mm)	Pod shape[b]	Auricles[c]	Pubescence[d]	Plant height (cm)	Mode of growth[e]	Foliage see Fig.:
6.5–7.0	4.9	0	1	35–40	E	20 I
9.9 (9.2–10.6)	7.6	0	0	60–68	A	20 F
8.7 (7.7–9.6)	6.2	2	1	37–51	A	20 K
6.3–9.7	5.4(3.7–7.4)	0–1	0–2	50–77	A	20 G
—	—	3	1	49	E	20 R
6.3 (6.1–6.9)	4.6	1	2	37–47	E	20 J
6.8–8.6	5.2–7.3	0–2	1–3	36–51	A–E	18 D–F
6.6 (5.9–6.9)	4.4	3	1	47–62	A–E	22 D–E
6.4 (5.8–7.1)	4.2	3	1	45–57	A–E	22 F
3.7 (3.3–4.0)	2.2	4	1	54–67	A–E	22 A
6.2 (5.8–6.6)	4.2	3	1	38–52	A–E	22 H–I
6.2 (5.5–6.6)	3.7	4	1	45–55	A–E	22 B–C
6.8 (6.2–7.2)	4.3	4	1	45–60	A–E	22 G
4.4 (4.0–4.5)	2.5	4	1	40–59	A–E	22 J
8.6 (8.1–9.6)	6.1	2	1	46–50	A–E	—
6.0–7.0	c. 3	3	0	c. 90	D–A	20 U

[d] 0 = stem glabrous; 1 = stem basally with few hairs or with a denser, but extremely fine pubescence; 2 = stem basally with scattered hairs; 3 = stem basally with a fairly dense and coarse pubescence.

[e] D = stem decumbent; A = stem ascending; E = stem erect, except for the very lowest part.

[f] Chromosome number unknown.

misunderstood, sometimes such showing traces of *R. amphibia* or *R. austriaca*. The failure of seed setting in *R. sylvestris* because of its self-incompatibility was often taken as an indication of hybrid nature, and the interpretation as *R. palustris* × *sylvestris* was often closest at hand. But also the unusual phenomenon of ripe pods in *R. sylvestris* has led to the apprehension of such plants as hybrids. In such cases the pod-shape was apparently interpreted as intermediate between *R. palustris* and *R. sylvestris*. Also *R. sylvestris* specimens with small petals as many clones at L. Mälaren, were ascribed to this hybrid combination.

The complete failure to cross *R. palustris* and *R. sylvestris* will make it necessary to conclude on hybrid nature from supposed intermediate morphology and distribution of the parent species. It seems quite clear that this hybrid is only rarely established and here only some evident cases will be referred. A very clear one is from Sweden, Hälsingland, Ljusdal par., Lake Borrsjön. From this locality two collections were distributed in Samuelsson's Pl. Suec. exs. (cf. Hultén 1946) as

No. 907 and No. 908, both named *Rorippa islandica* × *sylvestris* (cf. Lidman 1925). No. 907 is characterized as "*forma siliculis tenuibus*" and No. 908 as "*forma siliculis crassis*". Of the two No. 907 seems to be the species *R. sylvestris*, while No. 908 shows signs of an intermediary not only with respect to the pods, which often contain a small number of ripening seeds (cf. Table V and Fig. 20 U). About 85 % of the pollen grains are empty, but have well developed exine.

On a visit in 1963 to this locality, which is a sandy shore at a small lake, I found only specimens corresponding to No. 907, a clone of tetraploid *R. sylvestris* (J 1076). This was the only *Rorippa* biotype found besides *R. palustris*, which was also frequent on the shore (J 1077). The supposed hybrid clone was evidently extinct, but there seems to be no reason to doubt its formation on this place, where *R. sylvestris* is certainly a recent introduction. The hybridization would have taken place on the tetraploid level. In 1963 (31. VIII) only single pods of *R. sylvestris* showed tendencies to seed setting, in spite of its growing almost mixed with *R. palustris*. Either pollen dispersal from the autogamous *R. palustris* is of little importance or successful fertilizations of *R. sylvestris* by this pollen are rare events (cf. Ch. 5). In cultivation the clone J 1076 set seed in abundance.

Some other possible but much more uncertain cases will be cited. From eastern L. Mälaren there are a few collections which are likely to be this hybrid (Järfälla, Lövsta, 1915 and Lovö, Drottningholm, 1916, both Segerström LD). They show no traces of *R. amphibia*, set seeds to some extent and develop pods both broader and shorter than *R. sylvestris*. All the Danish collections supposed to be this hybrid in Pedersen (1958) lie within the normal variation range of *R. sylvestris*. No plausible Norwegian hybrids have been discovered, and those reported by Lid (1963) belong to *R. sylvestris* in the cases where herbarium specimens were controlled. Concerning Finland the clone from Helsingfors (Pl. Finl. exs. No. 1183, named *R. prostrata*, 1932 Hiitonen H, J 1114 and others), cited as the actual hybrid by Hiitonen (1947), has some features pointing towards *R. palustris* (e.g. the shape of fertile pods, and the small auricles, cf. Table V), but it is much closer to *R. sylvestris*. It may be some other tetraploid hybrid derivative of this species, perhaps with *R. austriaca* as the other component. Its occurrence around a large rail marshalling yard suggests independent introduction. From the British Isles some specimens exist that may be *R. palustris* × *sylvestris* but they do not permit any safe decision. The hybrid is not included in British plant lists (Druce 1928, Dandy 1958).

During the lapse of time genes from *R. palustris* might have contributed to the variation of *R. sylvestris*. But the hybrid between those species is evidently rarely realized and none of the frequent literature reports can be accepted unless supported by determinable herbarium material.

The *Rorippa austriaca* × *sylvestris* hybrids

The opinion that hybrids exist between *Rorippa austriaca* and *R. sylvestris* was probably first expressed by Reichenbach (1830–32) in connexion with his description of *Nasturtium astylon* (cf. Ch. 7) and more definitely by Neilreich (1852). During the same period forms of the actual hybrid series were described as species, notably by Tausch (1840), whose *Nasturtium armoracioides* is the current binary name for it (cf. Ch. 7). The relations between the species and varieties described by Tausch and others (cf. p. 111) were discussed by Čelakovský (1874), Borbás (1879*a*) and especially Fröhlich (1914). Błaszczyk (1953) studied the variability of the hybrid in the Kraków region. The hybrid is known from many localities in the regions of the rivers Vistula, Oder, Elbe and Danube (cf. Hegi 1958–63, Săvulescu 1955). In these regions both parent species grow spontaneously e.g. at rivers, and the hybrid is often recorded from such places, as well as from fields, roadsides and similar localities. I have not obtained any confirmation of the probable existence of the hybrid east of the area mentioned, i.e. in Russia, where the parent species also seem to be indigenous. Outside the area of indigenous *R. austriaca* the hybrid is only known as an introduced weed under conditions similar to those described below for Scandinavia.

Variability in Scandinavia

The morphology of the *R. austriaca* × *sylvestris* hybrids was touched upon above (p. 113) in a comparison with *R. amphibia* hybrids. Here chiefly such features which are of diagnostic value and illustrate variation will be treated. Morphological data of cultivated hybrids are given in Table V and in Ch. 8. The characters of special importance for distinguishing between these two series of *R. sylvestris* hybrids will of course be the same as used for separating *R. austriaca* and *R. amphibia*. The auricles of the cauline leaves are mostly nearly clasping or at least prominent (cf. Figs. 21, 22) in comparison with *R. amphibia* × *sylvestris*. Most of the pedicels of ripening pods are distinctly ascending, or in biotypes approaching *R. sylvestris*, sometimes horizontal. As a rule the cauline leaves have a more acute serration. Their segments are directed more forward and are often less well delimited from the central part of the lamina than in the *R. amphibia* × *sylvestris* hybrids (cf. Fig. 22). In *R. austriaca* and its hybrids the leaf-shape does not vary much according to the sequence along the shoot, as is the case in *R. amphibia* (cf. p. 105). There is a slight tendency to shorter petals, in comparison with fertile *R. amphibia* × *sylvestris* hybrids (cf. Table V). The interpretation of these plants as *R. austriaca* × *sylvestris* hybrids rests upon morphological comparisons with *Rorippa* species, distributional facts and crossability of the parent species (cf. Ch. 5). Unfortunately the progeny of this cross has not yet formed floral shoots.

According to Blom (1931) the Swedish material of *R. austriaca* × *sylvestris*

A. Indusy
1966

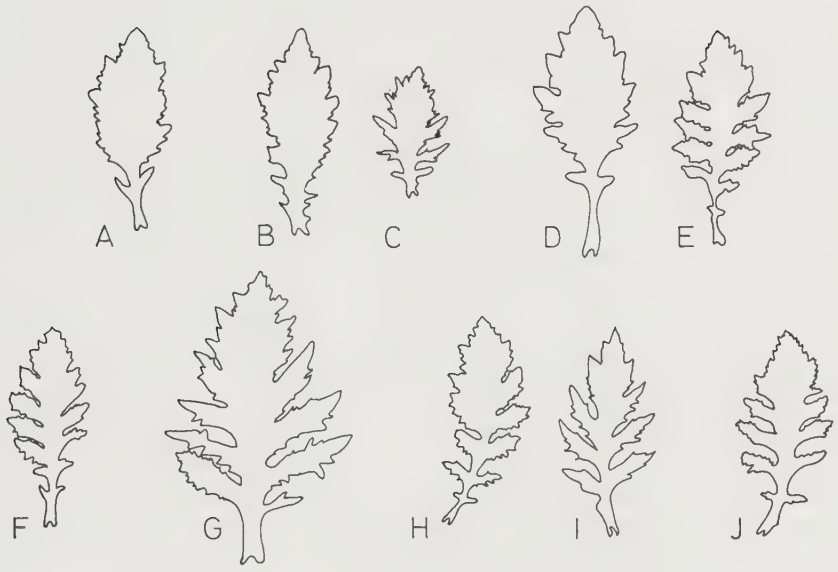

Fig. 22. Cauline leaves of *R. austriaca* × *sylvestris*. A: J 856. B–C: J 872. D–E: J 540. F: J 541. G: J 1090. H–I: J 868. J: J 1220. ½ ×.

could be fairly well assorted into two groups according to the shape of the leaves, which would be either little lobate or profoundly pinnatifid. In the larger material available today, and especially when the other Nordic countries are also considered, the variation of the cauline leaves seems rather continuous from one extreme to the other as seen from Fig. 22, where leaves from the clones in cultivation are illustrated. Blom's view may have been influenced by the fact that he regarded as the hybrid some collections of pure *R. austriaca* (Vg: Mariestad, cf. App. 6). Modifications are, however, of considerable importance here and affect particularly the variation between non-lobate and somewhat pinnatifid leaves. I collected the clone J 872 (cf. Fig. 21, 22, B–C) in the field with non-lobate cauline leaves, but more deeply serrate, a little broader and more petiolate than those of *R. austriaca*. A comparison between clones with seed setting pods indicates that pod-shape also shows a continuous variation pattern. The variation in this hybrid series displays the normal pattern of co-variation in parental characters, as was presented above for *R. amphibia* × *sylvestris*.

Like the parent species the hybrid *R. austriaca* × *sylvestris* forms vigorous subterranean root runners, from which adventitious shoots can arise (cf. Ch. 3). The hybrids are therefore equally apt to vegetative dispersal as its parents. Like weedy

Fig. 21. *R. austriaca* × *sylvestris*. Basal part of a specimen with a number of cut shoots, and major part of one flowering shoot. From a living plant (J 872), c. 0.4 ×

clones of *R. sylvestris* (cf. p. 102) *R. austriaca* × *sylvestris* clones can grow in dry places and it seems to surpass the species mentioned in tolerance to hard soil. Field-margins, roadsides and railway banks are among the typical habitats in Scandinavia.

The fertility of the Nordic *R. austriaca* × *sylvestris* clones is fairly good. Most specimens investigated have some good pollen grains, and many up to about 80 %, which is common for *R. sylvestris* clones (cf. Table V). All clones kept in cultivation set plenty of seeds in well developed pods when exposed to free pollination. Some successful crosses to *R. sylvestris* were referred to above (Ch. 5). The remark by Blom (op. cit.) about bad seed setting may be explained as based on specimens in isolated occurrences. This hybrid is obviously self-incompatible to the same extent as its parents, and therefore seeds are very rarely produced in Scandinavia.

Chromosome number and genesis

From eight Nordic occurrences of this hybrid the tetraploid chromosome number ($2n = 32$) was determined (see App. 1). These are the only counts so far reported. This number leads to some complication as to the genesis of this hybrid, since *R. austriaca* is only known as a diploid. Closest at hand is to imagine crosses between *R. austriaca* and hexaploid *R. sylvestris*. This cross did, however, not succeed experimentally (cf. Table III), and even if realized in nature it could hardly account for the existence of tetraploid hybrid clones morphologically rather close to *R. austriaca* and the rather continuous variation between the species described above. It must therefore be considered whether unreduced *R. austriaca* gametes may have functioned—in a primary cross or in back-crosses—or whether a tetraploid cytotype of *R. austriaca* may exist besides the diploid. The former suggestion does not imply that these events are common, for once tetraploid progeny was formed in a back-cross it could account for the formation of the numerous biotypes in later generations. As to the latter suggestion it should be remembered that so far only very few determinations of chromosome numbers have been made in *R. austriaca* (cf. App. 1 and Table I), and none of those are from the area where the species is indigenous. A much better knowledge of the situation in this area, especially S. E. Europe, is necessary before any conclusions can be drawn about the hybrid genesis.

Distributional history of the hybrid and R. austriaca in Scandinavia

Blom's (1931) statement that the Swedish occurrences of *R. austriaca* × *sylvestris* cannot be connected with the few isolated finds of *R. austriaca* is evidently valid for the whole of Scandinavia. There are many more finds of hybrids than of *R. austriaca* in all parts of this area (cf. App. 6 and 7). The hybrid must consequently have been introduced as such, and Blom's suggestion of dispersal as seeds with cereals from S. E. Europe seems very plausible with respect to the frequency and the fertility of the hybrids in those regions (cf. p. 139). Some finds at mills

and farms clearly indicate introduction by means of seeds (cf. App. 7). Most of the other finds were made close to important routes of communication, especially harbours and railways, and seeds would have been brought there by transports. To Domnarvet (Dalarna, Sweden) it was apparently spread with ore or scrap-iron from Russia or Germany (cf. Almquist 1949, p. 69). After a primary introduction the hybrid has apparently spread vegetatively, e.g. through soil transports in local areas, in the same way as *R. sylvestris* (cf. p. 103). Examples are available from N. W. Skåne, S. Halland, Bohuslän (Ljung par.) and Västergötland (the Borås region), all in Sweden (cf. App. 7). It is theoretically possible for new biotypes to be formed from crosses of the hybrid with tetraploid *R. sylvestris*, but no evidence of that exists. Where more than one biotype seems to exist from a local area a success for more than one seedling from the introduced seeds seems more probable.

For the species *R. austriaca* introduction with cereals is quite evident in still more cases, and the species is mentioned in Norway from mills renowned for their rich alien flora (Hanssen & Nordhagen 1930, Tambs Lyche 1931). On the whole its distribution pattern is similar to that of the hybrid (see App. 6) although in most parts of Scandinavia *R. austriaca* does not persist in a locality, being perhaps more susceptible to the climate. Only in Denmark has the species endured for longer times in some places and probably also spread somewhat locally, e.g. at Skagen (N. Jutland), where it is reported growing on sand dunes, at Kvissel in Vendsyssel (N. Jutland), where it was collected in both 1921 and 1946, and at N. Nebel (W. Jutland), where it is growing rather frequently at a railway at least since 1951 (= J 1552). A find close to the last-mentioned (Kvong) is a possible case of local dispersal. In W. Norway (especially Hordaland) it is or has been constant at some mills and has been dispersed from those particularly with cereals used as poultry foods (cf. App. 6).

At least for the hybrid a considerable increase in frequency is evident in Scandinavia during the 20th century. The first documented find is from Oslo in 1905, and there are several collections from this city during the 1910ths and afterwards. The first Swedish collections are from about the same time (see App. 7), while the first Danish finds were made somewhat later. In Finland both the hybrid and *R. austriaca* first appeared—in the 1920-ies and 1930-ies—chiefly in the south-eastern provinces and mostly at railways (cf. e.g. Fagerström 1939–40, 1942), which suggests introduction from Russia.

After Blom's compilation in 1931 of all Swedish finds known by then, the hybrid has been discovered in quite a few new localities, though mostly in provinces previously known to house it. But particularly in Norway and to some degree in Finland it was also found in many new areas during the 1940-ies and 1950-ies. This reminds rather much of the situation in *R. sylvestris* if the differences in frequency are disregarded. The hybrid has in recent times sometimes been found as a garden weed (cf. App. 7). Like *R. sylvestris*—and in contrast to *R.*

austriaca—it seems to have good chances of persisting in an area once it is introduced. From Scandinavia there are, however, very few examples of the hybrid growing at shores (Skårman 1942) as is often reported from Central Europe, and in no case can it be stated that naturalization has taken place.

So far the hybrid *R. austriaca* × *sylvestris* has not been recorded for the British Isles, and no specimen was revealed in the herbaria penetrated. *R. austriaca* is known, however, from quite a few places (cf. Perring & Walters 1962, Map No. 102/6).

VII. NOMENCLATURE AND TYPIFICATIONS

Generic and sectional names

Most of the European species treated in this work were originally included in the genus *Sisymbrium* (Linnaeus 1753 and others, see below), and there they remained in most works till the early 19th century. After the splitting of that genus, a number of names have been used for the actual group of taxa, the most important being *Radicula* Hill, Brit. herbal (1756), *Rorippa* Scopoli, Fl. Carn. (1760) and *Nasturtium* R. Brown ap. Aiton fil., Hort. Kew. (1812). The first name, revived by Druce (1906), should be rejected according to the International Code (1966) Art. 20 (cf. Schinz & Thellung 1909). The name *Rorippa*, which was first used in binary combinations by Besser (1822) was introduced by Scopoli (1760) in a work where binary nomenclature is not employed. Scopoli included in his genus only one species, which according to the three synonyms, e.g. Linnaeus (1737*b*), clearly is *Rorippa sylvestris*. Hence that would be the type-species (holotype) of the genus *Rorippa*. In a recent work, Abrams (1944), *Rorippa amphibia* is given as the generic type. This is not in accordance with Scopoli (1760) and must be left without consideration. The name *Nasturtium*, used in various senses by 18th century authors, was conserved as a generic name in the sense of R. Brown ap. Aiton fil. (1812) against the names *Cardaminum* Moench, Meth. Pl. (1794) and *Beaumerta* Gaertn., Mey. & Scherb., Fl. Wett. (1800). The type species is *Nasturtium officinale* R. Br. (= *Rorippa nasturtium-aquaticum* (L.) Hayek). During the 19th century *Nasturtium* was taken in a broad sense and used also for species of the section *Rorippa* and so also by Schulz (1936), who did not observe that *Nasturtium* is not conserved against *Rorippa* (cf. Mansfeld 1938, Hylander 1945). Therefore the correct generic name for sect. *Rorippa* will be *Rorippa*, irrespective of whether or not *Nasturtium officinale* is included in the same genus (see Ch. 1). In the former case the last-mentioned species and its allies constitute a section for which *Cardaminum* seems to be the correct name. Other generic names used for certain species are *Brachiolobos* Allioni, Fl. Pedem. (1785)—formerly also name of the type-section (sect. *Brachylobos* DC., Reg. Veg. Syst. Nat. (1821))—*Tetrapoma* and *Tetracellion*, both Turczaninow ex Fischer & Meyer, Ind. Sem. Horti Petrop. 1 (1835), cf. p. 33. Many larger genera of the *Cruciferae* have occasionally been apprehended as to comprise *Rorippa* species, as will be clear from the lists of synonyms in Ch. 8.

About the source and spelling of the name *Rorippa*, see Sprague (1930).

Specific names

The three species *Rorippa amphibia*, *R. palustris* and *R. sylvestris* are all nomenclaturally based upon names given by Linnaeus (1753). The epithets of the two former are both found within the same Linnaean species, *Sisymbrium amphibium*, which therefore must be critically examined as to its components.

Rorippa amphibia and Rorippa palustris. Sisymbrium amphibium is one of the rather few cases in Species Plantarum (1753), where Linnaeus has split a species without any remainder into three co-ordinated varieties. They were called *α palustre*, *β aquaticum* and, by an error corrected in later editions, "*δ*" *terrestre*. Under each a number of synonyms are given. A study of those will clarify, at least for the varieties *α* and *β*, Linnaei concept of their circumscription.

The first synonym under *α palustre* is the phrase-name used for the species No. 551 in Flora Suecica (1745), and the third (last) one is followed by citations to Bauhinus (1620, 1623) and to the species No. 262 in Linnaei Flora Lapponica (1737*a*). In the latter work is also found a similar phrase-name—the first—"*Sisymbrium aquaticum, foliis in profundas lacinias divisis*", which bears a citation to Tournefort (1719). Citations to all the four works mentioned are also found under No. 551 in Fl. Suec. (1745). Some of them are clearly linked with the plant now known as *R. palustris*. The illustration cited in Bauhinus (1620) is a characteristic *R. palustris*, and the species No. 262 in Fl. Lapp. (1737*a*), said to grow "*in sylvis Lapponiae paludosis*" can already from geographical reasons be no other than *R. palustris*. There is also a specimen of *R. palustris* in the Linnaean herbarium in Paris, apparently collected during his Laponian journey (see below). Thus two of the four synonyms (the second and fourth) under No. 551 in Fl. Suec. (1745) are definitely linked with *R. palustris*. The first synonym is more uncertain. The passage "*foliis infimis capillaceis*" does not accord with *R. palustris* but with *R. amphibia* and its hybrids. It is cited from Hortus Cliffortianus (1737*b*), but there is no corresponding specimen in the Clifford herbarium. It seems most probable that this phrase-name does not primarily refer to a plant of *R. palustris*, but under this entry in Hort. Cliff. (1737*b*) are found the citations from Bauhinus (1620) and Tournefort (1719) mentioned above. It has not been possible to relate the Tournefort name to *R. palustris* with full evidence (see below). The third synonym in Fl. Suec. (1745) I have not verified but its wording is so close to the second and fourth that it certainly means the same plant. There are some more synonyms given in the Linnaean works mentioned antedating Spec. Plant. (1753), which I have not been able to prove to belong to *R. palustris*, although they may do so. Returning to Spec. Plant. (1753) this means that the first and third synonyms under *α palustre* concern *R. palustris*, while the second (from Hort. Cliff.) is uncertain.

Under var. *β aquaticum* the first phrase-name cited is from Hortus Cliffortianus

(1737*b*)—the species No. 3 under *Sisymbrium*—and its relation to *R. amphibia* is clear through a sheet in the Clifford herbarium (see below). The two further synonyms are from Bauhinus (1620, 1623). That from Bauhinus (1620) is linked with *R. amphibia* through the illustration in Tab. 38. There is no reason to suspect any element of var. *aquaticum* in Species Plantarum or under the corresponding phrase-name in earlier Linnaean works not to fall within *R. amphibia* in the modern sense.

Under var. "*δ*" *terrestre* two synonyms are cited. The first is from Vaillant (1727) where it is regarded as a variety of the Tournefort plant cited in Hortus Cliffortianus under the *Sisymbrium* species No. 3, which is our *R. amphibia*. The second synonym is from Haller (1742). To judge from the descriptions it seems most probable that these names were given to some *R. amphibia* hybrids. Linnaeus had obviously no personal experience of his variety *terrestre* and none of the two synonyms are found in his earlier works, nor in Flora Suecica ed. 2 (1755).

The "*nomen specificum legitimum*" standing for the aggregate species, *Sisymbrium amphibium*, lacks citations and was evidently created new in Species Plantarum (1753) to cover the heterogeneous material. As evident from the above account Linnaeus had earlier (in Hortus Cliffortianus (1737*b*) and Flora Suecica (1745)) regarded the varieties *α* and *β* as separate species, with essentially the same circumscriptions. He knew both from the Swedish flora, but just in Flora Suecica (1745) he expressed doubts as to their specific rank, thus anticipating their reduction to varieties. From the evidence presented I find it clear that for the var. *palustre* Linnaeus had primarily the plant now called *Rorippa palustris* in mind. Although he perhaps to some extent confused our *R. palustris* and *R. amphibia* in Species Plantarum (1753), he even later sometimes recognized the former, as is clear from a list in Herbationes Upsalienses (Linnaeus 1756), where *Sisymbrium palustre* appears as a *nomen nudum*. It seems therefore not justifiable to follow the view held first by E. Fries (1828) and accepted by Schinz & Thellung (1909) that all three varieties of *Sisymbrium amphibium* should be interpreted as falling within *R. amphibia*.

A special comment is needed to explain why the trivial name *Sisymbrium amphibium* should be typified upon var. *aquaticum*, a case earlier touched on by Sprague (1955) and Santesson (1966). In Species Plantarum none of the three varieties is mentioned as typical, but in Flora Suecica, ed. 2 (1755) Linnaeus transposed *α* and *β*, thus placing var. *aquaticum* next to the specific name. In the synonym list he even omitted any special sign for this variety, but employed the letter *β* for var. *palustre*. The alteration of the text from Species Plantarum must imply that Linnaeus regarded var. *aquaticum* as typical for *Sisymbrium amphibium*,[1] and upon that interpretation rests the possibility of using the names

[1] A note by Linnaeus in his own copy of Flora Suecica (1745) at the Linnaean Society, London, underlines this view. In the species No. 551 (our *R. palustris*) he has changed the

Rorippa amphibia and *R. palustris* at the same time in their present senses. If the view of Schinz & Thellung (1909) is accepted *R. amphibia* will of course remain valid, but it is very doubtful whether the epithet *palustris* can be used at all. The first one known to make a valid combination *Sisymbrium palustre* is namely Pollich (1777) and he clearly based his species upon the var. *palustre* in Flora Suecica, ed. 2 (1755).

Between the years 1753 and 1777 some designations occasionally regarded as binary names were created. They must be shown not to be so, or *Sisymbrium palustre* (L.) Pollich would become a later homonym resp. synonym of those. Garsault (1767) gave the name *Sisymbrium palustre* without citing any authorities to a plant that to judge from the rather poor illustration (Plate 550) approaches *Rorippa amphibia*. But Garsault (1767) is, already from examples within the genus *Sisymbrium*, clearly a work where binary nomenclature is not consistently employed, an opinion earlier expressed by Hylander (1938). Garsault's names should therefore be rejected (Internat. Code 1966, Art. 23).

According to Grande (1928) another synonym of *Rorippa palustris* exists, viz. "*Sisymbrium Radicula*" Grimm 1773. Grimm (1773) cited as a synonym a phrase-name from Haller (1768) "RADICULA *foliis pinnatis, pinnis dentatis, petalis calyce brevioribus*", a species to which Haller to judge from localities cited attributed material of both *R. palustris* and *R. islandica*. Grimm's citation of this name under *Sisymbrium*, "*Sisymbrium Radicula foliis ...*" cannot possibly be interpreted as though he made a new binary name, "*Sisymbrium Radicula*". Epithets of binary names were moreover by Grimm (op. cit.) in similar cases always put within brackets.

The Linnaean herbarium in London does not provide type specimens of *Sisymbrium amphibium* var. *aquaticum* or var. *palustre*. The London specimen of the former, No. 836:9, marked by Linnaeus as "*Sisymbrium amphibium*, 3" was included in the herbarium between 1755 and 1763 (Jackson 1912). It carries no reference to var. *aquaticum* and consists of three separate parts. The Clifford herbarium, however, contains a well preserved and characteristic specimen (about the upper half of a plant), which from notations on the sheet is connected with the third species under *Sisymbrium* in Hortus Cliffortianus, which is what in 1753 was called var. *aquaticum*.[1] This will hence be the lectotype of *Sisymbrium amphibium* var. *aquaticum* and consequently also of the specific name. Its origin is unknown. The "type locality" would be the places given in Hortus Cliffortianus for

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last sentence, which expresses that No. 551 is easy to discern from No. 550 (our *R. amphibia*), to "*sola varietas a hoc*". He evidently this time regarded No. 550 as the typical plant, No. 551 as the variety.

[1] About the connexions in general between Hortus Cliffortianus and the Clifford herbarium see Rendle (1923) and Stearn (1957).

the corresponding species viz. "*frequens per Sueciam, Germaniam, Belgium, Angliam*".

For var. *palustre* the only specimen discovered with close association to Linnaeus is the one present in the collection at Institut de France, Paris. This collection, the main part of which was brought together by Linnaeus during his Laponian journey in 1732, was listed and commented upon by Th. M. Fries (1861) and has later been discussed by Alston (1957) and Stearn (1957). A photograph of the sheet was placed at my disposal. Two portions of plants are mounted on the sheet, but they may be from the same specimen: the upper half of a shoot probably just beginning to flower, and a large leaf, obviously from the basal part of the stem. There seems to be some damage due to insects, which have in particular affected the inflorescence. Hence only the vegetative parts can be studied but the plant is definitely a *R. palustris*. It does certainly not belong to *R. islandica* s.str., nor to any of the American subspecies of *R. palustris*, not only because of its origin but also to judge from observable characters. The sheet carries the numbers of the species in Flora Lapponica (262) and of the actual page (214). The former type of numbers, which as a rule are present in the collection, are considered as having been written by Linnaeus (Fries 1861, Alston 1957). On the sheet also the Tournefort name quoted in Flora Lapponica is written, probably by Burmann (see Alston op. cit.), to whom the collection was originally addressed. This specimen I select as the lectotype for *Sisymbrium amphibium* var. *palustre*. Except this one I have only traced one more specimen with a possible connexion to Linnaei description but also in bad condition. It belongs to the collection of Vaillant (in P), and carries Tournefort's phrase-name in a handwriting reported to be close to the one found also in Tournefort specimens. If at all, this specimen is very indirectly linked with Linnaeus.

Rorippa sylvestris. For *R. sylvestris* the case is comparatively simple. The entry in Species Plantarum (1753) is cited from Hortus Cliffortianus (1737*b*). In the Clifford herbarium a corresponding sheet is present, carrying two very similar shoots with pods and flowers, most probably from the same individual, which should be selected as the lectotype. As "type localities" for *R. sylvestris* it would be most advantageous to cite the places listed in Hortus Cliffortianus, viz. "*circa Genevam; Montbelgardum; Porentruum. ... Basileam, Stultgardiam &c. in Belgio*", which are more accurately defined and fully covered by those of Species Plantarum.

It should be emphasized here that there is no specimen of *R. sylvestris* in the London Linnaean herbarium linked with Species Plantarum. The specimen cited by Davis (1965) is not *R. sylvestris* but *R. pyrenaica* (Lam.) Rchb. (No. 836:6, on which "*sylvestre*" is written by Linnaeus; see Lindberg 1958, p. 81). According to a label it was collected in 1753 near St. Gotthard, and cannot have been considered during the work upon Species Plantarum. It is obviously a misidentifica-

tion by Linnaeus, who had probably no recent experience of the species in question (cf. p. 100).

Rorippa islandica. The basionym *Sisymbrium islandicum* was first employed in Oeder's Flora Danica, Vol. 3 (1768). The validity of Oeder's name has been repeatedly discussed, due to the question as to whether or not binary nomenclature was used in his work (Fernald 1929, 1940, Becherer 1930, Mansfeld 1939, Sprague 1939, Hylander 1945). After the discovery by Butters & Abbe (1940) that Oeder's name was unequivocally validated through Murray (1773), it is of little importance in this case to settle the question concerning Oeder's volume. In Murray (op. cit.) there is a quotation of Oeder's whole phrase-name and a reference to the corresponding plate. From Murray's description, which in fact is a comparison with *R. sylvestris*, it is clear that he identified with Oeder's species a specimen of *R. palustris* and he thus introduced the wide sense of Oeder's name current until now.

Sisymbrium islandicum is typified by plate No. 409 in Flora Danica. The illustration shows many of the features distinguishing *R. islandica* from *R. palustris*. The origin of Oeder's plant is certainly in Iceland, since Oeder obtained seeds collected by J. G. Koenig during his Icelandic journey 1764–65, and these gave rise to luxuriant plants in the Botanical garden in Copenhagen. The plate is apparently drawn from one of those cultivated plants, which explains its well-nourished appearance with numerous shoots from the base. I have not managed to find any herbarium specimens connected with Oeder's plate.

Ball (1961) observed that there is in the Linnaean herbarium, London, a specimen of "*R. islandica*" labelled *Sisymbrium pyrenaicum*. This specimen (No. 836:4) is, in fact, *R. islandica* s.str. and emanates probably from the Alps. It is fairly well in accordance with the description of *S. pyrenaicum* L. Syst. ed. 10 (1759), which is, however, an illegitimate name being a later homonym of *S. pyrenaicum* L. ex Loefl. Iter hisp. (1758) (see further Ball op. cit.). The Linnaean specimen is therefore without importance for the nomenclature of *R. islandica*.

Rorippa austriaca. The basionym is *Nasturtium austriacum* Crantz (1762). Keller (1943) called attention to the existence at BP of a specimen collected by Crantz at one of the localities cited with the description, viz. Nusdorf. Though only in flower it is in full accordance with Tab. II in Crantz (1762) and it would be the holotype.

Some synonyms. Here some comments will be made on names frequently cited as synonyms of those treated above. On the whole only names concerning European material are considered. Only those needing special comments and not treated in other connexions (cf. pp. 62, 74) will be mentioned here.

Sisymbrium hybridum Thuillier, Fl. env. Paris (1799) is generally regarded as a synonym of *Rorippa palustris* s.lat. The largest collection of authentic Thuillier

specimens is found in the Delessert herbarium in Geneva, and should be regarded as containing types of Thuillier's new taxa (cf. Lasègue 1845). The specimen of *Sisymbrium hybridum* there belongs to *R. palustris* s.str. Thuillier (op. cit.) also recorded *Sisymbrium pusillum* Villars from the Paris region, but the corresponding specimen is clearly *R. sylvestris*.

Myagrum pumilum Lamarck, Encycl. méth. (1785) is according to the descriptions and Lamarck's remarks a species of the *Rorippa islandica* group, but probably not *R. palustris* which Lamarck (op. cit.) included as *Myagrum palustre*. There is no indication of its origin. No authentic specimens were found in P–LA at the investigations kindly undertaken after my inquiry.

Sisymbrium terrestre Withering, Bot. Arr. Br. Pl. (1787) and *Roripa nasturtioides* Spach, Hist. Vég. Phan. (1838) are both *nomina superflua*, since in the first case *Sisymbrium palustre* (L.) Pollich (1777) is cited, in the second besides this one several older binary names. Also *Sisymbrium vulgare* Persoon, Syn. Pl. (1807) is a *nom. superfluum*, since *S. sylvestre* L. is cited with the description. Moench (1794) also contributed superfluous names, viz. *Radicula pinnata* for which he gave *Sisymbrium sylvestre* L. as a synonym, and *Radicula lancifolia*, for which he cited one of the synonyms on which *Sisymbrium amphibium* L., em. L. 1755 is based.

Binary hybrid names

The use of binary names for hybrids seems justifiable in such cases where a recognizable hybrid, little variable and fairly well isolated from its parent species, has gained some distribution of its own. Such a case is *Rorippa* × *sterilis* Airy-Shaw (*R. microphylla* × *nasturtium-aquaticum*) in sect. *Cardaminum*. For the hybrids of sect. *Rorippa* treated here binary nomenclature seems, however, partly unnecessary and troublesome to employ, owing to the difficulties to interpret the names given to hybrid forms. For the most important hybrids, *R. amphibia* × *sylvestris* and *R. austriaca* × *sylvestris*, the binary nomenclature will, however, be discussed.

Rorippa × *prostrata* (Bergeret) Schinz & Thell. The oldest binary name known for any of the hybrids within sect. *Rorippa* is *Myagrum prostratum* Bergeret, Phytonomatotechnie Vol. 3, p. 149 (1784) (= *Rorippa* × *prostrata* (Berg.) Schinz & Thellung). The type should be the corresponding plate in Bergeret (op. cit.), also reproduced, though somewhat altered and named *Brachiolobos sylvestris* in Allioni (1785). The illustration may represent a *R. amphibia* × *sylvestris* hybrid and so it was interpreted by Schinz & Thellung (1913), but especially the acute sepals, the short styles and the ascending pedicels are atypical. The latter feature suggests rather a *R. austriaca* × *sylvestris* hybrid. The name is much used in Central European literature, but the identity of Bergeret's plant seems too dubious to make this justified.

Rorippa × *anceps* (Wg) Rchb. As discussed in Ch. 6 *Sisymbrium anceps* Wahlenberg, Fl. Upsal. (1820), is most probably based upon material representing *R. amphibia* × *sylvestris*. The description is also in accordance with such an interpretation. Some confusion may arise from his statement of "*foliis subauriculatis*", but small auricles are not rarely present in *R. amphibia* × *sylvestris* hybrids, nor in the parent species. I have seen only one specimen (in UPS) collected by Wahlenberg before 1820 that he attributed to his new species. The original label runs: "*Sisymbrium amphibium* var. *foliis subauricul.* Upsala nedvid ån på Kungsängen d. 9 Julii 1818". According to a label by Ahlberg it was placed in Wahlenberg's herbarium as *Nasturtium anceps*. This specimen, which I choose as the lectotype of *Sisymbrium anceps* Wg, has very small auricles at some leaves only, and deeply pinnatisect leaves with narrow segments (Fig. 19 Q; cf. Table V for further data). It agrees completely with *R. amphibia* × *sylvestris* both from L. Mälaren and other regions.

The name has been used in various senses partly according to the varying interpretation of the Uppsala hybrids, and the taxon has been circumscribed in very different ways (see Borbás 1882, Blom 1931, Hiitonen 1947, Hylander 1961). The name has been proposed to be rejected as ambiguous (Čelakovský 1874), but since it is doubtless based upon the Uppsala hybrids this seems inappropriate. But *Rorippa anceps* Fuss, Fl. Transsilv. Exc. (1866) is apparently a later homonym, as it was erected without any reference to Wahlenberg. It may also represent a *R. amphibia* × *sylvestris* hybrid. Since the combination *Rorippa anceps* with citation of Wahlenberg was in fact used by Reichenbach (1837–38) in the comments to Ic. Flor. Germ.—but not in the plates—*R. anceps* (Wg) Rchb. has priority under *Rorippa*. It would be the correct binary name for *R. amphibia* × *sylvestris*, if *R.* × *prostrata* is not accepted.

Rorippa × *astylis* (Rchb.) Rchb. Reichenbach (1830–32) described a plant that he considered to be the hybrid *R. austriaca* × *sylvestris* and gave to it the name *Nasturtium astylon*. The plate in Reichenbach (1837–38) shows a plant with a habit approaching *R. austriaca*, but, as the epithet indicates, with pods devoid of the styles, which in the supposed parent species and their hybrid are generally long and slender. It represents probably a female sterile clone with misformed gynecia, but from the plate it is not unequivocally clear that it is *R. austriaca* × *sylvestris*. I prefer therefore not to take up this name, an opinion shared by Tomšovic (in litt.) and which can be based upon the Internat. Code (1966) Art. 71, if the Reichenbach plant is regarded as a monstrosity.

Rorippa × *armoracioides* (Tausch) Fuss. Tausch (1840) described a number of *Rorippa* taxa from Bohemia (cf. p. 111) and gave some of them specific rank. One is *Nasturtium armoracioides* which according to Tausch's description and discus-

sion would be *Rorippa austriaca* × *sylvestris*. I have seen some authentic specimens collected at the R. Moldau and preserved in PRC, which clearly are this hybrid. Another of the Tausch species, *Nasturtium barbaraeoides*, includes, at least partly, *R. austriaca* × *sylvestris* hybrids. The authentic material seen by me approaches *R. sylvestris* and the *R. austriaca* characters are little pronounced and somewhat uncertain.

Since I have not studied all available Tausch collections and since research is being performed in Prague, I will not decide about the typification of *R.* × *armoracioides*. After the rejection of *R.* × *astylis* I find it most probable, however, that *R.* × *armoracioides* is the correct binary name for *R. austriaca* × *sylvestris*.

VIII. CONSPECTUS OF TAXA

The Conspectus is intended to summarize in a monographic way facts given in the previous account, but some data on morphology and distribution are only presented here. The N. W. European taxa are treated at first hand, but their subspecies from other areas are also included in smaller print. Species supposed to be especially close to those treated are mentioned in brief. The key, which has been elaborated with respect to N. W. European material only, tries to make possible determinations also of the hybrids. It should be stressed that it can only be valid for hybrid derivatives more or less intermediate between the parent species and with correlated character variation. Rare and aberrant combinations, whose interpretation is always somewhat uncertain, might be evaluated only from comparisons between the descriptions.

Abbreviations of European countries and Nordic provinces are explained in p. 167.

The synonymy is carried through only for names applied to material from Europe and eastern North America. Names below the rank of subspecies are treated only when they are of special interest, e.g. the varieties of *Nasturtium palustre* s.lat. that can be identified with *R. islandica*.

"General distribution" includes only evidence from herbarium material or from maps that are cited in each case, but no exhaustive investigation was made into this matter. Unverified literature reports have not been considered.

Key to the N.W. European species and hybrids

Petals and sepals of about equal length. Rooting stem portions and root runners absent.

Pods 2–3 times as long as their pedicels. Sepals shorter than 1.6 mm. Seeds very finely colliculate. *R. islandica*, p. 155

Pods not more than c. 2 times as long as their pedicles. Sepals longer than 1.6 mm. Seeds more coarsely colliculate. *R. palustris*, p. 157

Petals at least 1.5 times as long as the sepals. Rooting stem portions or root runners present.

Cauline leaves with prominent, often nearly clasping auricles.

Leaves not lobate. Pods spheroid. *R. austriaca*, p. 163

Leaves lobate. Pods ellipsoid – oblong.

Petals shorter than 3.5 mm. Cauline leaves about 4 times as long as broad, rather coarsely serrate. *R. amphibia* × *palustris*, p. 162

Petals usually longer than 3.5 mm. Cauline leaves 2–3 times as long as broad, usually acutely serrate. *R. austriaca* × *sylvestris*, p. 164

Cauline leaves with no or inconspicuous auricles.

Upper cauline leaves not lobate. Pods spheroid – ellipsoid. *R. amphibia*, p. 161

Upper cauline leaves lobate.

Cauline leaves deeply pinnatisect. Terminal segment short and narrow. Styles shorter than 1.2 mm.

Ripe pods not broader than 1.2 mm; unfertilized ovaries linear. Petals nearly always longer than 3.0 mm. *R. sylvestris*, p. 160

Ripe pods 1.3–1.5 mm broad; unfertilized ovaries narrowly ellipsoid. Petals shorter than 3.0 mm. *R. palustris* × *sylvestris*, p. 160

Cauline leaves pinnatifid – pinnatisect. Terminal segment 1/4–2/3 of the total leaf-length, broad. Styles nearly always longer than 1.2 mm. Ripe pods at least c. 1.5 mm broad.

In fruit with most pedicels deflexed from the base.

R. amphibia × *sylvestris*, p. 163

In fruit with ascending – horizontal pedicels.

R. austriaca × *sylvestris*, p. 164

Rorippa islandica* (Oeder ex Murray) Borbás, A Balaton Flórája, 2, p. 392 (1900),** quoad basion., **ssp. *islandica

Sisymbrium islandicum Oeder ex Murray, N. Comment. Soc. Scient. Gotting. 3, p. 81 (1773). *Sisymbrium*, (islandicum?) *siliquis brevibus declinatis, foliis lyratopinnatis, foliolis ovalibus dentatis* Oeder, Fl. Danica, Vol. 3, Fasc. 7, p. 8 (1768). Coll. orig.: Islandia. Tab. No. 409 in Oeder, Fl. Danica, 1768 (Holotypus) [vide p. 150].
Radicula islandica (Oeder ex Murray) Druce, Rep. Bot. Soc. Exch. Club Brit. Isles, 3, p. 9 (1912)—nom. rejic. [vide p. 145].
Sisymbrium pusillum Villar, Fl. delphinalis, p. 69 (1785). Coll. orig.: Gallia, Hautes-Alpes, Mt. Gondran. Tab. No. 39 in Villars, Hist. Pl. Dauphiné, 3, 1789 (Holotypus) [vide p. 62].—*Nasturtium palustre* (L.) DC. *β pusillum* (Vill.) De Candolle, Regni Veg. Syst. Nat. 2, p. 192 (1821).
Nasturtium palustre (L.) DC. var. *montanum* Brügger, Zeitschr. Ferdinand. Tirol u. Vorarlberg 3. Folge, 9:5, p. 26 (1860). Coll. orig.: Helvetia, Graubünden, "Lenzerheide, 4600'", 1849, C. Brügger (CHUR, lectotypus!) [vide p. 62].
Nasturtium palustre (L.) DC. var. *longesiliquosa* (!) Lange, Conspectus Fl. Groenlandicae p. 47 (1880). Coll. orig.: Groenlandia, Tunugdliarfik, 60°50′, J. Vahl (C, lectotypus!) [vide p. 58].
Nasturtium palustre (L.) DC. var. *gelidum* Murr, Deutsche bot. Monatsschr. 15, p. 76 (1897). Coll. orig.: Italia, "Tirol, Seiseralpen, Mahlknechthütte". Tab. No. 4 in Murr 1897, p. 100.
? *Sisymbrium pyrenaicum* L. Syst. ed. 10, 2, p. 1132 (1759)—[non *S. pyrenaicum* L. ex Loefl. Iter Hisp. p. 304, descr. 61 (1758)] [vide p. 150].
? *Myagrum pumilum* Lamarck, Encycl. méth. Botanique, 1, part 2, p. 572 (1785).—*Cardamine palustris* (L.) O. Kuntze *β pumila* (Lam.) O. Kuntze, Rev. Gen. Pl. 1, p. 25 (1891).

Annual, rarely slightly perennial with a fine tap root. Main shoot branched from just above the primordial leaves or slightly higher up into 2–12 flowering stems,

which are usually branched, decumbent – ascending and 4–30 (40) cm long. Leaves pure green, sometimes anthocyanic. Leaf-rosette sometimes persisting. Cauline leaves slender, 3–7 times as long as broad, deeply pinnatisect with 3–5 pairs of lateral segments and a short, narrow terminal segment (Fig. 5). Leaf-segments finely serrate – entire. Petioles indistinctly winged with no or very inconspicuous auricles. Racemes few – numerous, when fruiting often in one marked plane and strongly divaricating from the axis. (Plate V, C–D, Fig. 6.).

Petals pale – pure yellow 1.0–1.5 (1.7) mm long; sepals 1.1–1.5 (1.6) mm long (Fig. 2). Longer stamens 1.2–1.7 mm with 0.3–0.5 mm long anthers. Pods richly seed setting, 6–12 mm long, 2–3 mm broad, about 2–3 times as long as the patent – deflexed, usually <4 mm long, pedicels (Fig. 4), often somewhat torulose and, when young, often broader near the base. Valves markedly thin looking, opening almost to the point of attachment on the pedicel (Plate V, A). Style 0.3–0.7 mm long, c. 0.3 mm broad; stigma indistinctly capitate. Seeds pure – light brown, 0.6–0.9 mm long, very finely colliculate. Seed epidermal cells 20–32 (35) μ wide, 22–32 (36) μ high (Fig. 1). Glabrous except very sparse hairs at the leaf-bases and sepals.

CHROMOSOME NUMBER. $2n=16$ (Table I, App. 1, Figs. 7, 8).

HABITATS. Open sandy – muddy shores of lakes, streams and pools, also at ditches etc. Hemerophilous (pp. 57–62).

DISTRIBUTION IN N.W. EUROPE. *Hb* W. Galway. *Br* Isle of Man, Wigtown, Midlothian, Orkney Islands. *Is. No* Nrd. (Fig. 7, App. 2.)

GENERAL DISTRIBUTION. EUROPE: France (Alps and Pyrenees), Switzerland, Italy. N. AMERICA: Greenland. (Fig. 7, App. 2.)

MAP. Gröntved 1942, Fig. 100 (Iceland).

Rorippa islandica (Oeder ex Murray) Borbás ssp. *dogadovae* (Tzvelev) Jonsell n.stat.

Rorippa dogadovae Tzvelev, Botaniczeskie materialy gerb. im. Komarova 18, p. 98 (1957). Coll. orig.: U.R.S.S., Kazakhstan, Pavlodar, ad flumen Irtysh. A. Dogadova & N. Tzvelev No. 852 [Herb. Fl. U.R.S.S No. 4115] (LE, holotypus. Isotypi in BM! K! S!).

[?] *Nasturtium palustre* (L.) DC. *β orientale* Zinger, Sbornik svedeniy o flore Sredney Rossii, p. 55 (1885). Coll. orig.: non vidi [vide p. 64].

Very similar to ssp. *islandica*, but leaves usually more dissected with deeply incised lateral segments (Fig. 5, G–H) and pods mostly somewhat shorter. Seed epidermal cells 24–32 μ wide and 42–52 μ high (Fig. 1).

DISTRIBUTION: U.S.S.R., at the Rivers Volga, Ural, Ob, Irtysh, Yenisey and Aley (Fig. 7, App. 2).

In western N. America taxa of close affinity to *R. islandica*, especially *R. curvipes* Greene and allied species (cf. p. 65).

***Rorippa palustris* (L.) Besser, Enum. Pl. Volhyniae, p. 27 (1822),**
ut Roripa, **ssp. *palustris***

Sisymbrium amphibium L. α *palustre* L. Sp. Pl. p. 657 (1753). Coll. orig.: Suecia (?), "Lapponia", C. Linnaeus (Institut de France, Paris, lectotypus/photogr!/) [vide p. 149].
Sisymbrium palustre (L.) Pollich, Hist. plant. Palat. elect. 2, p. 230 (1777)—[non *S. palustre* Garsault, Descr. vert. usages pl. p. 514 (1767), nom. non rite publ., vide p. 148].—*Myagrum palustre* {L.} Lamarck[1], Encycl. méth. Botanique, 1, part 2, p. 572 (1785).—*Radicula palustris* (L.) Moench, Meth. plant. p. 263 (1794), nom. rejic. [vide p. 145].—*Caroli-Gmelina palustris* (L.) Gaertner, Meyer & Scherbius, Fl. Wett. 2, p. 470 (1800).—*Brachyolobos palustris* {L.} Clairville, Man. Herb. p. 218 (1811).—*Nasturtium palustre* (L.) DeCandolle, Regni Veg. Syst. Nat. 2, p. 191 (1821)—[non Crantz, Classis Crucif. p. 81 (1769)].—*Cardamine palustris* (L.) O. Kuntze, Rev. Gen. Pl. 1, p. 24 (1891).
Sisymbrium amphibium L. p.p., em. Miller, Gard. Dict. ed. 8 (1768) non s. em. L. Fl. Suec. ed. 2, p. 231 (1755) [vide p. 147].
Sisymbrium terrestre Withering, Bot. Arr. Br. Pl. ed. 2, 2, p. 692 (1787)—nom. illeg. superfl. [vide p. 151].—*Nasturtium terrestre* (With.) R. Brown ap. Aiton fil, Hort. Kew. ed. 2, 4, p. 110 (1812), [non *N. terrestre* (L.) Tausch, Flora 45, p. 711 (1840)]—nom. illeg.—*Roripa terrestris* (With.) Fuss, Fl. Transsilv. Exc. p. 47 (1866), quoad basion.—nom. illeg.
Sisymbrium hybridum Thuillier, Fl. env. Paris, ed. 2, p. 331 (1799). Coll. orig.: in G, herb. Delessert, lectotypus! [vide p. 150]—[non *Brachylobus hybridus* Schur, Enum. Pl. Transsilv. p. 40 (1866) nec *Rorippa hybrida* Klokov, Botan. Zhurnal (Kiev) 5, p. 30 (1948)].
Roripa nasturtioides Spach, Hist. Vég. Phan. 6, p. 506 (1838)—nom. illeg. superfl. [vide p. 151].
["*Sisymbrium radicula* Grimm (1773)" s. Grande, Bull. ort. bot. Napoli 8, p. 127 (1926), vide p. 148.]

Annual – perennial, though not long-lived, with tap root. Main shoot (5) 10–110 cm high, usually erect from the base, either unbranched besides in the inflorescence or (in well-developed specimens) branching only after reaching about 10 cm length or more, but forming buds at the base from which after hibernation ascending – erect secondary shoots may protrude. Leaves pure green – light green, often anthocyanic. Leaf-rosette mostly ephemeral. Cauline leaves 3–5 times as long as broad, deeply pinnatisect, with (0) 2–6 pairs of ± lanceolate lateral segments and the terminal segment ± elliptic of 1/3–1/2 of the total leaf-length (Fig. 5, I–N). Petioles winged, but sometimes very short as the leaves may be nearly sessile. Auricles usually distinct but not clasping. Racemes in the top only, or few – numerous from the axils of upper leaves. (Plate V, E–F.)

Petals pale – pure yellow (1.5) 1.7–2.6 (2.8) mm long; sepals green 1.6–2.4 mm long (Fig. 2). Longer stamens 1.7–2.5 mm long with 0.3–0.6 mm long anthers.

[1] {L.} means that the Linnaean trivial name was not cited, only one or more of the phrase-names given in Linnaei synonymy.

Pods richly seed setting, (4) 5–10 (12) mm long, 1.7–3.0 mm broad, ellipsoid – oblong and curved, from somewhat shorter to twice as long as the horizontal – deflexed pedicels (Fig. 4). Valves usually of firm consistency, reaching only to 0.3–0.5 mm from the point of attachment of the pedicel. (Plate V, B.) Styles 0.4–1.0 (1.2) mm long; stigmata capitate. Seeds pure – light brown, 0.6–0.9 mm long, finely colliculate; epidermal cells 35–50 (55) μ wide, 25–45 μ high (Fig. 1). Nearly glabrous (in Europe, cf. p. 76 ff.), with scattered hairs along petioles and at sepals, rarely in the lower parts of the stem.

CHROMOSOME NUMBER. $2n = 32$ (Table I, App. 1, Fig. 8).

HABITATS. Open shores (gravelly – sandy – muddy) of lakes, streams, ponds, ditches; also in moist tramped ground. Sometimes on sea-wrack. Strongly hemerophilous. Adventitious at roads, railways, in harbours etc. (cf. p. 70 f.).

DISTRIBUTION IN N.W. EUROPE. *Hb* Eire, N. Ireland. *Br* Engl., Scotl., Wales (App. 3 and Perring & Walters 1962). *Da* all prov. (except Lang?; Pedersen 1958). *Su* all prov. *No* all prov. *Fe* all prov. *Rs* Fennoscandian part, probably all prov.

GENERAL DISTRIBUTION. EUROPE: lowland regions exc. the Arctic, rare in the Mediterranean region. ASIA: Siberia, Central Asia, Caucasus. /Not clarif. as to ssp: Himalayas, N. India, China, Korea, Japan/. N. AMERICA: Alaska, Canada, U.S.A. Rec. introd.: Greenland. /Not clarif. as to ssp: C. AMERICA (introduced?): Cuba, Haiti, Mexico. S. AMERICA (introd.): Brazil, Colombia. AFRICA (introd.): e.g. Egypt, Ethiopia. AUSTRALIA (probably introd. and naturalized, cf. p. 73): New S. Wales, Queensland, Victoria, S. Australia, Tasmania, New Zealand./

Rorippa palustris (L.) Besser ssp. *fernaldiana* (Butters & Abbe) Jonsell n.comb.

Rorippa islandica (Oeder ex Murray) Borb. var. *fernaldiana* Butters & Abbe, Rhodora 42, p. 28 (1940). Coll. orig.: America borealis, Maine, Ft. Fairfield, 1893, M. L. Fernald (MIN, holotypus! Isotypus in GH!)—[non *Nasturtium palustre* (L.) DC. var. *microcarpum* Regel, Tent. Fl. Ussur., p. 20 (1861). Coll. orig.: U.R.S.S., "Amur, zwischen Sianka u. Köurmi, auf sandiglehmigen Inseln, häufigst", 1855, Maximovicz (LE, typus!, vide p. 76).]

Very indistinctly delimited from ssp. *palustris* and ssp. *occidentalis* and in some respects from ssp. *hispida* (cf. p. 82), but markedly tall, robust and erect. Cauline leaves somewhat thick, rather narrow with no or 1–2(3) lanceolate lateral segments and an elliptic terminal segment of more than half the length of the lamina, practically sessile usually with prominent auricles (Fig. 5, O). Pods ovoid – oblong, (3)4–6 mm long, shorter than or about equalling the pedicels. From nearly glabrous to rather densly pubescent on lower parts of the stem, on petioles and leaves.

CHROMOSOME NUMBER. $2n = 32$ (App. 1).

DISTRIBUTION. N. AMERICA: at least northern U.S.A., Canada (exc. the Pacific region); in Alaska obscure in relation to ssp. *palustris* and ssp. *occidentalis*.

Rorippa palustris (L.) Besser ssp. _occidentalis_ (Watson in A. Gray) Abrams, Ill. Fl. Pacific States 2, p. 278 (1944)

Nasturtium terrestre (With.) R. Br. var. *occidentale* Watson in A. Gray, Syn. Fl. N. America 1:1, p. 148 (1895). Coll. orig.: America borealis, Alaska, Shumagin Islands, Popov I., W. H. Dall (GH, typus sec. Hultén 1945); "Brit. Columbia, Lyall, Macoun, Lower Columbia Valley, Hall, Suksdorf, Howell" (vide A. Gray op. cit.).

Tall and robust. Leaves usually with large terminal segments and 2–4 pairs of lateral segments. Pods large, oblong and curved, c. 8–13 mm long and 2.5–3 mm broad, often markedly clavate. Completely glabrous.

DISTRIBUTION. N. AMERICA: At least Pacific coast regions from S. Alaska to California, perhaps wider.

Rorippa palustris (L.) Besser ssp. _hispida_ (Desvaux) Jonsell n.stat.

Brachilobus hispidus Desvaux, Journal de Botanique 3, p. 183 (1814). Coll. orig.: America borealis, Pennsylvania, Palisot de Beauvois (G, holotypus!).

Rorippa hispida (Desv.) Britton, Mem. Torr. Bot. Cl. 5, p. 169 (1894).—*Nasturtium palustre* var. *hispidum* (Desv.) A. Gray, Manual of Bot. ed. 2, p. 30 (1856) —*Rorippa palustris* var. *hispida* (Desv.) Rydberg, Bot. surv. Neb. rep. 3, p. 26 (1894).—*Rorippa islandica* var. *hispida* (Desv.) Butters & Abbe, Rhodora 42, p. 26 (1940).

Indistinctly delimited from ssp. *palustris* and in some respects from ssp. *fernaldiana* (cf. p. 74), but cauline leaves with 4–6 rather acute lateral segments and a ±rhomboid terminal one, not longer than about a third of the leaf (Fig. 5, P–Q). Pods nearly spheroid – ovoid, 3–5 mm long, distinctly shorter than the pedicels. Stigmata mostly not capitate. Usually densely pubescent: stem (always below, often even in the racemes) and leaves with short, simple, stiff hairs.

CHROMOSOME NUMBER. $2n = 32$ (App. 3).

DISTRIBUTION. N. AMERICA: at least N.E. U.S.A. and E. Canada; in W. Canada and Alaska less pronounced.

MAPS. *R. palustris.* Hultén 1950 No. 925 (the Nordic area). Pedersen 1958 Fig. 43 (*Da*). Hård av Segerstad 1935 No. 207 (*Su* Dls) and 1952 No. 135 (*Su* Vrm). Sterner 1938 No. 146 (*Su* Öl). Englund 1942 p. 272 (*Su* Gtl). Holmgren 1942 p. 24 (*Su* Bl). Benum 1958 No. 309 (*No* Trs). Suominen 1962 No. 133 (*Fe* St, Karkku par.). Fl. Murmansk. Obl. 1956 No. 109 (*Rs* Lps, Lt, Lim, Lm, Lv, Lp, parts of Ks, Kk). Perring & Walters 1962 No. 102/4 (as to the majority of records, cf. p. 66. British Isles). Christiansen 1953 No. 1339 (*Ge* Schleswig-Holstein). Busch 1913–31 p. 206 (Eurasia). Grossheim 1950 No. 232 (*U.S.S.R.*: Caucasus). Hultén 1928 No. 436 (*U.S.S.R.*: Kamtchatka), 1937*a* No. 255 (*Alaska*: Aleutian Islands) and 1945 Nos. 634 a, 634 b, 635 a (*Alaska. Canada*: Yukon). Wiggins & Thomas 1962 p. 356 (*Alaska*: Arctic Slope). Raup 1947 Pl. 26 (*Canada*: S.W. Mackenzie Distr.). Deam 1940 Nos. 1016 and 1017 (*U.S.A.*: Indiana). Beal & Monson 1954 p. 64 (*U.S.A.*: Iowa). Jones & Fuller 1955 No. 586 (*U.S.A.*: Illinois). Patman & Iltis 1961 Nos. 36, 37 (*U.S.A.*: Wisconsin). Steyermark 1963 p. 760 (*U.S.A.*: Missouri). Lakela 1965 p. 462 (*U.S.A.*: N.E. Minnesota).

Of close affinity are *R. barbareifolia* (Beringian area) and the *R. curvipes* group (western N. America) [cf. p. 84 f.].

HYBRIDS:

R. palustris* × *sylvestris

Perennial. Shoots ascending. Cauline leaves ± deeply pinnatisect. Petioles with distinct auricles. Petals c. 2.5–3.2 mm long; sepals c. 2.0 mm long. Pods with irregular or failing seed setting, attaining 1.3–1.5 mm width, on ascending horizontal pedicels. Styles c. 1 mm. Glabrous, except auricles and sepals. (Table V.)

VERIFIED FROM: *Su* Upl?, Hls.

R. amphibia × *palustris* (p. 162).

***Rorippa sylvestris* (L.) Besser, Enum. Pl. Volhyniae, p. 27 (1822),** ut Roripa

Sisymbrium sylvestre L. Sp. Pl. p. 657 (1753). Coll. orig.: BM, Hortus Siccus Cliffortianus, lectotypus! [vide p. 149].
Brachiolobos sylvestris (L.) Allioni, Fl. Pedem. 1, p. 278 (1785) quoad basion. [vide p. 151].—*Caroli-Gmelina sylvestris* (L.) Gaertner, Meyer & Scherbius, Fl. Wett. 2, p. 470 (1800).—*Nasturtium sylvestre* (L.) R. Br. ap. Aiton fil., Hort. Kew. ed. 2, 4, p. 110 (1812).—*Sisymbrella sylvestris* (L.) Spach, Hist. Vég. Phan. 6, p. 425 (1838).—*Radicula sylvestris* (L.) Druce, Ann. Scott. Nat. Hist. 1906, p. 219, nom. rejic. [vide p. 145].
Radicula pinnata Moench, Meth. Pl. p. 263 (1794)—nom. illeg. superfl. [vide p. 151].
Sisymbrium vulgare Persoon, Syn. Pl. 2, p. 196 (1807)—nom. illeg. superfl. [vide p. 151].
Nasturtium rivulare Reichenbach, Iconogr. bot. Tab. No. DXVII (711) et Comment. p. 14 (1828). Coll. orig.: Germania, Sachsen, "zwischen Laubegast und Pilnitz" Tab. cit.

Perennial. With far-creeping, branching root runners from which adventitious shoots arise, often mat-forming. Stems 15–60 (90) cm high, mostly branching already from the base, decumbent – ascending – nearly erect. Leaves pure and often dark green, sometimes with a bluish tinge. Basal leaf-rosette disappearing after the first year. Cauline leaves about twice as long as broad, deeply pinnatisect with 4–6 pairs of lateral segments, which are lanceolate – rhomboid, entire – sparsely serrate or deeply cut (Fig. 12); terminal segments lanceolate – oblong with apex acute – rounded 1/5–1/4 of the total leaf-length (Fig. 12). Petioles nearly always distinct, auricles small or (usually) absent. Racemes numerous, rather dense and short (in comp. with *R. amphibia*) with straight – flexuous axis, in the top and from the axils of central and upper leaves. (Plates IX–XI.)

Petals light – pure yellow (2.2) 2.8–5.5 mm long (Figs. 10, 11); sepals green – greenish yellow 1.8–3.0 mm long. Longer stamens 1.7–3.5 mm long with 0.7–1.0 mm long anthers. Pods rarely seed setting (cf. p. 35 f.),9–22 mm long 1.0–1.2 mm broad (Fig. 10), linear, often curved. Unfertilized ovaries develop to 4–8 (10) mm length. Pedicels horizontal – ascending, 4–10 (12) mm long. Styles 0.5–1.0 (1.2) mm long, 0.2–0.3 mm broad. Seeds reddish brown, 0.6–0.8 mm long, finely colliculate. Nearly glabrous, single hairs on petioles and sepals. (Figs. 10, 11.)

CHROMOSOME NUMBERS. $2n = 32$, 40, 48 (Table I, App. 1, Fig. 13).

HABITATS. Gravelly – sandy open shores of lakes and streams, strongly hemerophilous. Adventitious in gardens, at roads, in harbours; formerly on ballast.

DISTRIBUTION IN N.W. EUROPE. *Hb* Eire, N. Ireland. *Br* Engl., Wales, Scotl. (Perring & Walters 1962). *Is*. *Da* all prov. exc. Lang, Mön. *Su* all prov. exc. Hrj, LL, TL. *No* all prov. exc. Fnm. *Fe* all prov. exc. Ik, Ks, Lk, Le, Li, Lps. *Rs* Fennoscandian part: Kol, Kpoc. (App. 4, Figs. 13, 16.)

GENERAL DISTRIBUTION. EUROPE: most lowland regions. ASIA: Turkey, Caucasus. AFRICA: Mediterranean region? N. AMERICA (introduced): Canada, U.S.A.

MAPS. Hultén 1950 No. 927 (the Nordic area). Pedersen 1958 Fig. 44 (*Da*). Hård av Segerstad 1924 No. 78 (S. Sweden). Holmgren 1942 p. 24 (*Su* Bl). Almquist 1929 No. 269 (*Su* Upl) and 1948 Fig. 4 (*Su* Upl, parts of Srm, Vsm). Benum 1958 No. 310 (*No* Trs). Perring & Walters 1962 No. 102/3 (British Isles). Lawalrée 1955–57 Fig. 74 (*Be*). Grossheim 1950 No. 230 (*U.S.S.R.*: Caucasus). Stuckey 1966*a* p. 364 (*U.S.A.*). Deam 1940 No. 1018 (*U.S.A.*: Indiana). Patman & Iltis 1961 No. 34 (*U.S.A.*: Wisconsin). Steyermark 1963 No. 1086 (*U.S.A.*: Missouri). Lakela 1965 p. 462 (*U.S.A.*: N.E. Minnesota). Jones & Fuller 1955 No. 587 (*U.S.A.*: Illinois).

In S.E. Europe and Turkey related taxa, not sufficiently known: *R. kerneri* Menyh., *R. brachycarpa* (C. A. Mey.) Hayek, *R. prolifera* (Heuff.) Neilr. and *R. aurea* (Boiss.) Huber-Morath.

HYBRIDS:

R. amphibia × *sylvestris* (p. 163), *R. austriaca* × *sylvestris* (p. 164) and *R. palustris* × *sylvestris* (p. 160).

***Rorippa amphibia* (L.) Besser, Enum. Pl. Volhyniae, p. 27 (1822),** ut Roripa

Sisymbrium amphibium L. Sp. Pl. p. 657 (1753) p.p., saltem quoad β aquaticum, em. L. Fl. Suec. p. 231 (1755)—non s. em. Miller, Gard. Dict. ed. 8 (1768). Coll. orig.:BM, Hortus Siccus Cliffortianus, lectotypus! [vide p. 148].

Brachiolobos amphibius (L.) Allioni, Fl. Pedem. 1, p. 278 (1785).—*Nasturtium amphibium* (L.) R. Br. ap. Aiton fil., Hort. Kew. ed. 2, 4, p. 110 (1812).—*Myagrum amphibium* (L.) Loiseleur, Fl. Gall. ed. 2, 2, p. 50 (1828).—*Armoracia amphibia* (L.) Petermann, Fl. Lips. p. 477 (1838).—*Cochlearia amphibia* (L.) Ledebour, Fl. Ross. 1, p. 160 (1842).—*Radicula amphibia* (L.) Druce, Ann. Scott. Nat. Hist. 1906, p. 220, nom. rejic. [vide p. 145].

Sisymbrium aquaticum {L.} Miller, Gard. Dict. ed. 8 (1768).—*Myagrum aquaticum* (L.) Lamarck, Fl. fr. 2, p. 483 (1778).—*Nasturtium aquaticum* (L.) Wallroth, Sched. crit. Fl. Hal. p. 371 (1822)—[non Wahlenberg, Fl. Suec. p. 418 (1824)].

[*Sisymbrium aquaticum* Garsault, Descr. vert. usages pl. p. 324 (1767)—nom. non rite publ., vide p. 148.]

[*Sisymbrium palustre* Garsault, ibidem,—nom. non rite publ., vide p. 148.]

Radicula lancifolia Moench, Meth. Pl. p. 262 (1794)—nom. illeg. superfl. [vide p. 151].

Sisymbrium stoloniferum J. S. & C. B. Presl, Fl. Čech. p. 137 (1819), quoad descr., coll. orig. non vidi.

Nasturtium natans DC. Regni Veg. Syst. Nat. 2, p. 198 (1821). Coll. orig.: Tab. 15 in Delessert, Ic. selectae plant. 2 (1823).—*Cochlearia natans* (DC.) C. A. Meyer in Ledebour, Fl. Alt. 3, p. 90 (1831).

Perennial. Root runners rarely developed, but with superficial or submerged, prostrate, rooting basal stem portions on which new axillary shoots are formed as leaf-rosettes from which floral stems may ascend the following year. Stems (20) 40–120 cm high, mostly (if not submerged) with a basal, ephemeral rosette of lyriform leaves. The primary, usually non-persisting, cauline leaves pectinately pinnatisect–pinnatifid. Upper cauline leaves non-lobate, elliptic–oblanceolate (sometimes lyriform), 4–8 times as long as broad, serrate or denticulate with no or small auricles. Lower leaves petioled, upper sessile. Racemes numerous, in the top and from the axils of upper leaves, elongate and rather loose.

Petals pure–orange yellow (3.5) 4.0–5.5 mm long; sepals 2.3–2.7 (3.0) mm long, often greenish yellow. Longer stamens 3.0–4.0 mm with 0.7–1.0 mm long anthers. Pods rather rarely seed setting (cf. p. 35 f.), with few seeds (2.5) 3–5 (6) mm long, 1.7–2.5 (3.0) mm broad, ovoid–oblong, much shorter than the pedicels, which are mostly deflexed from the base. Styles 1.0–2.5 mm long, c. 0.2 mm broad. Seeds reddish brown, 0.7–1.0 mm long, finely colliculate, often somewhat marginate. Almost glabrous–rather densely pubescent in young shoots and leaves, esp. the lower side.

CHROMOSOME NUMBERS. $2n = 16$, 32 (Table I, App. 1, Fig. 14).

HABITATS. On shores and in shallow water of eutrophic–mesotrophic lakes (often in floating drift of reeds), at rivers and ponds. Hemerophilous but not apophytic (cf. p. 109 f.).

DISTRIBUTION IN N.W. EUROPE. *Hb* Eire, N. Ireland. *Br* Engl., Wales, probably occasional: Scotl. (Perring & Walters 1962). *Da* all prov. (Pedersen 1958, cf. p. 110). *Su* Sk, Bl, Klm, Ög, Vg, Hl, Srm, Upl, Vsm. *No* Akh, AuAgd (ballast). *Fe* St, Ta, Tb, Ob. *Rs* Fennoscandian part: Kol, Kon. (cf. p. 109).

GENERAL DISTRIBUTION. EUROPE: widely distr. in lowlands, rare in the Mediterranean region. ASIA: Turkey, Near East, Caucasus, Central Asia, Siberia (not E. of R. Lena). N. AMERICA (introduced): Canada, U.S.A.

MAPS. Hultén 1950 No. 924 and Hylander 1960 p. 274 (the Nordic area). Pedersen 1958 Fig. 42 (*Da*). Hård av Segerstad 1924 No. 77 (S. Sweden). Almquist 1929 No. 268 (*Su* Upl). Suominen 1962 No. 132 (*Fe* St, Karkku par.). Perring & Walters 1962 No. 102/5 (British Isles). Lawalrée 1955–57 Fig. 76 (*Be*). Busch 1913–31 p. 218 (Eurasia). Meusel, Jäger & Weinert 1965, Karten p. 160 (Eurasia). Grossheim 1950 No. 235 (*U.S.S.R.*: Caucasus). Marie-Victorin 1930, p. 4 (*Canada*: Quebec).

HYBRIDS:

Rorippa amphibia* × *palustris

Perennial. Stems ascending, vigorous. Cauline leaves about 4 times as long as broad, pinnatifid with 4–6 pairs of later alsegments. Auricles prominent, nearly

clasping. Petals 2.5–3.5 mm long; sepals 1.8–2.5 mm long. Seed setting failing – irregular. Pods ellipsoid – oblong, usually on deflexed pedicels. Styles 0.7–1.5 mm. Nearly glabrous. (Table V.)

CHROMOSOME NUMBERS. $2n = 24$, 32 (Table I).

VERIFIED FROM: *Br* Surrey, Gloucestershire (cf. p. 131).

Rorippa amphibia* × *sylvestris

Rorippa × *anceps* (Wg) Rchb., Comment. Ic. Fl. Germ. et Helv. 2, p. 15 (1837–38) pro sp.—*Sisymbrium anceps* Wahlenberg, Fl. Upsal. p. 223 (1820). Coll. orig.: Suecia, Uppland, Upsala, Kungsängen, 1818 (UPS, lectotypus!) [vide p. 152].

Perennial. Often with vigorous root runners forming adventitious shoots. Shoots also from superficial prostrate basal stem portions. Stems decumbent – ascending, 35–100 cm high. Cauline leaves dark green 2.5–4 times as long as broad, finely serrate – entire, in the basal part of the stem often pectinately divided, higher up pinnatifid – pinnatisect with 2–7 pairs of lateral segments, which are mostly distinctly delimited from the central lamina, and a terminal segment c. 1/4–2/3 of the total leaf-length. Auricles small or absent. Petals 3.5–5.0 (5.5) mm long (sometimes considerably shorter cf. p. 118); sepals 2.0–3.0 (3.8) mm long. Seed setting often rich; pods (3) 5–10 mm long, 1.2–2.0 (2.5) mm broad, ellipsoid – oblong, usually on deflexed pedicels. Styles (0.8) 1.2–2.5 (3.0) mm. Glabrous or with a fine, rather dense pubescence in basal parts of the stem. (Plates VI–VII, Table V, Fig. 17.)

CHROMOSOME NUMBERS. $2n = 32$, 40 (App. 1).

VERIFIED FROM: *Hb* Eire, N. Ireland. *Br* Engl., Wales. *Da* Jl, Sj, Brnh. *Su* Sk, Ög, Ner, Srm, Upl, Vsm. *Fe* Ob. (App. 5, Fig. 16).

***Rorippa austriaca* (Crantz) Besser, Enum. Pl. Volhyniae, p. 103 (1822),** ut Roripa

Nasturtium austriacum Crantz, Stirpium Austr. Fasc. 1, p. 15 (1762). Coll. orig.: Austria, "Nusdorf via" (BP, holotypus!) [vide p. 150].

Myagrum austriacum (Cr.) Jacquin, Fl. Austr. 2, Tab. 111 (1774).—*Camelina austriaca* (Cr.) Persoon, Syn. Pl. 2, p. 191 (1807).—*Cochlearia austriaca* (Cr.) Ledebour, Fl. Ross. 1, p. 160 (1842).—*Brachylobus austriacus* (Cr.) Schur, Enum. Pl. Transsilv. p. 41 (1866).

Myagrum crantii Vitman, Summa Plant. 4, p. 9 (1790)—nom. illeg. superfl.

Perennial. With root runners from which adventitious shoots arise. Stems 40–100 cm high, ascending – nearly erect, branched in the upper parts. Leaves dull green – bluish green. Basal leaf-rosette disappearing after the first year. Cauline leaves 3–4 (5) times as long as broad, undivided, entire – serrate, sessile with clasping auricles. Racemes numerous, in the top and from the upper leaf axils, more compact than in *R. amphibia*.

Petals yellow 3.0–4.0 (4.5) mm long; sepals 2.0–2.5 mm long. Longer stamens 2.3–3.0 mm, with 0.6–0.8 mm long anthers. Pods rarely seed setting (cf. p. 35), c. 3 mm long and 2.5–3.0 mm broad, spheroid – ovoid, much shorter than the pedicels, which are horizontal – ascending, but sometimes with the outer half deflexed. Unfertilized ovaries spheroid, c. 2 mm. Styles 1.0–2.0 mm long, 0.1–0.2 mm broad. Seeds reddish brown, 0.7–0.9 mm finely colliculate. Nearly glabrous, but with a very fine pubescence in the basal part of the stem.

CHROMOSOME NUMBER. $2n = 16$ (Table I, App. 1).

HABITATS (in N.W. Europe). Harbours, at mills and silos, road sides, railways.

DISTRIBUTION IN N.W. EUROPE. *Br* Engl., Wales (Perring & Walters 1962). *Da* Jl, Fyn, Sj. *Su* Sk, Klm, Vg, Gbg, Srm. *No* Östf, Akh, Busk, Tel, VAgd, Rog, Hrd, STrd. *Fe* Ta, Ik. (App. 6.)

GENERAL DISTRIBUTION. EUROPE (indigenous or naturalized): S. E. Germany, S. Poland, Czechoslovakia, Austria, Hungary, N. Balkan, S. and C. Russia. Introduced in Western and the rest of Central Europe. ASIA: Turkey, Caucasus, Central Asia. N. AMERICA (introduced): U.S.A.

MAPS. Perring & Walters 1962 No. 102/6 (British Isles). Grossheim 1950 No. 235 (*U.S.S.R.*: Caucasus).

HYBRID:

Rorippa austriaca* × *sylvestris

Rorippa × *armoracioides* (Tausch) Fuss, Fl. Transsilv. Exc. p. 47 (1866) pro sp.— *Nasturtium armoracioides* Tausch, Flora 45, p. 707 (1840) [vide p. 152].

Perennial. With root runners from which adventitious shoots arise, often in dense clumps, not like mats. Stems 40–80 cm high, branching already from the base, ascending. Cauline leaves 2–3 times as long as broad, usually acutely serrate, pinnatifid – pinnatisect with 1–4 pairs of lateral segments (rarely undivided and deeply serrate), which (especially the proximal pair) are rather indistinctly delimited from the central part of the lamina. Terminal segments 1/4–2/3 of the total leaf-length. Petioles distinct, auricles prominent – clasping. Petals 3.0–4.5 mm long; sepals 1.8–3.0 mm long. Seed setting may be rich; pods (3.0) 3.5–9.0 mm long, 1.5–2.0 mm broad, ellipsoid – oblong on horizontal – ascending pedicels. Styles (0.8) 1.2–1.5 mm long. Nearly glabrous, but basal part of the stem with a very fine pubescence. (Fig. 21, Table V.)

CHROMOSOME NUMBER. $2n = 32$ (App. 1).

VERIFIED FROM (introduced): *Da* Jl, Fyn?, Sj. *Su* Sk, Bl, Sm?, Gtl, Vg, Hl, Gbg, Bh, Upl, Dlr, Hls, Mpd, Ång. *No* Östf, Akh, Opl, Busk, Vestf, Tel, VAgd, Hrd. *Fe* Ab, Nyl, St, Ta, Sa, Ka, Kl, Ik. (App. 7.)

SUMMARY

The present study aims at elucidating the multifarious variation met with in the N.W. European species of sect. *Rorippa* and its taxonomic significance and, for some taxa spread as weeds, the distributional history in Scandinavia. The investigations are based upon herbarium material and living plants, especially from Scandinavia, and combine data from morphology, chromosomal cytology, distribution, ecology and crossing experiments.

R. islandica s.lat. consists in N.W. Europe of two species, the diploid *R. islandica* with a restricted Atlantic distribution and the tetraploid widespread *R. palustris*. *R. islandica* is also distributed in the Alps, the Pyrenees and Greenland and as ssp. *dogadovae* in S.E. Russia—W. Siberia. It is of close affinity to some taxa in western N. America, the *R. curvipes* complex. *R. islandica* and *R. palustris* are separated by a series of morphological characters, among which are the anatomy of pod-valves and seed-coat. No intermediate populations are known.

R. palustris is in N.W. Europe rather little variable except in N. Fennoscandia, where pod-shape and leaf-shape vary rather much. This suggests the partial amalgamation in this region of an indigenous, primarily alluvial population on the one hand, and a population of introduced weeds on the other.

In N. America *R. palustris* is much more variable than in Europe and some exclusively N. American subspecies (ssp. *fernaldiana*, ssp. *hispida* and ssp. *occidentalis*) can be discerned. There are, however, no clear-cut differences between European and N. American material and much of the latter should be attributed to the European ssp. *palustris*.

R. islandica and *R. palustris* belong to a chiefly N. American group of taxa, the "*R. islandica* group" with short-lived, markedly autogamous plants.

R. sylvestris, which is morphologically highly variable in many characters, forms strongly self-incompatible clones. They are usually tetra- or hexaploid, rarely pentaploid. The cytotypes are not morphologically recognizable throughout, but there are tendencies to larger organs in the hexaploids. The pollen is in most clones of normal colpate type, but in some it is throughout of a highly divergent "nonaperturate" type. This pollen is unfunctionable and consists usually of PMCs where the meioses have been interrupted. Specimens with such pollen are partly recognizable by gross-morphological characters.

In Scandinavia there is generally only one *R. sylvestris* clone present in a locality and hence new biotypes are rarely formed. By means of vegetative dispersal

a clone may obtain wide distribution. It is to some extent possible to discern distinct groups of clones: one tetraploid of slender shore clones; one hexaploid of vigorous weeds; another hexaploid of weeds with nonaperturate pollen. These groups are extremes, and most clones are in various respects intermediate between them. No taxonomic subdivision of N.W. European *R. sylvestris* is therefore justifiable. Aneuploid *R. sylvestris* clones were obtained from crosses but have not been found in nature.

R. sylvestris is probably not even on shores indigenous in Scandinavia, though it was earliest known from such localities where it seems always to be tetraploid. It has expanded strongly as an anthropochore. During the 19th century it spread especially to harbours, e.g. with ballast, in recent times especially with garden soil. The older shore populations have not contributed to this expansion.

R. amphibia is in Scandinavia only tetraploid, but diploids are known from W. Europe. No taxonomic subdivision according to the cytotypes seems possible. It is pronouncedly self-incompatible and occurs in clones that are chiefly propagated and dispersed vegetatively. It does not occur as a weed outside the shores but it might have been introduced to some of its Scandinavian localities.

R. austriaca, only known as diploid, is in Scandinavia a rare alien persisting only in some Danish and Norwegian localities. It is chiefly introduced with cereals.

Between tetraploid *R. amphibia* and tetra- and hexaploid *R. sylvestris* hybrids are easily formed both experimentally and in nature. They are tetra- and pentaploid resp. and usually fertile. Tetraploid hybrids back- and intercross, and hence whole series of biotypes arise. This situation is in Scandinavia found at L. Mälaren and in parts of Skåne. Pentaploid hybrids, in Scandinavia only known from Skåne, produce aneuploid offspring, which has not been found in nature. The *R. amphibia* × *sylvestris* hybrids do not spread as weeds. Tetraploid *R. sylvestris* shows often signs of introgression in regions where it grows together with tetraploid *R. amphibia*.

Hybrids between *R. amphibia* and *R. palustris* were obtained from crosses but are rarely formed in nature. They have not been verified from Scandinavia but from England.

R. palustris × *sylvestris* is very rarely established in nature and was not obtained experimentally.

R. austriaca × *sylvestris* occurs in tetraploid, self-incompatible but fertile clones that have been independently introduced to Scandinavia chiefly as seeds with cereals. It was not known from Scandinavia before 1900 but has expanded in later times and persists in many places. Triploid hybrids between *R. austriaca* and *R. sylvestris* were obtained from crosses.

EXPLANATIONS OF ABBREVIATIONS

European countries (the abbreviations follow Flora Europaea 1964).

Au	Austria
Be	Belgium
Br	Great Britain
Cz	Czechoslovakia
Da	Denmark
Fe	Finland
Ga	France
Ge	Germany
Hb	Ireland
He	Switzerland
Ho	Netherlands
Hu	Hungary
Is	Iceland
Ju	Yugoslavia
Lu	Portugal
No	Norway
Po	Poland
Rm	Rumania
Rs	Russia
Su	Sweden

Nordic provinces (the abbreviations follow Hylander 1953).

Denmark:

Brnh	Bornholm
Flst	Falster
Fyn	Fyn
Jl	Jutland (Jylland)
Lang	Langeland
Loll	Lolland
Mön	Mön
Sj	Sjælland (Zealand)

Finland:

Ab	Regio aboënsis
Al	Alandia (Åland)
Ik	Isthmus karelicus
Ka	Karelia australis
Kb	Karelia borealis
Kl	Karelia ladogensis
Ks	Kuusamo
Le	Lapponia enontekensis
Li	Lapponia inarensis
Lk	Lapponia kemensis
Lps	Lapponia petsamoënsis
Nyl	Nylandia (Nyland)
Oa	Ostrobottnia australis
Ob	Ostrobottnia borealis
Ok	Ostrobottnia kajanensis
Om	Ostrobottnia media
Sa	Savonia australis
Sb	Savonia borealis
St	Satakunta
Ta	Tavastia australis
Tb	Tavastia borealis

Norway:

Akh	Akershus
AuAgd	Aust-Agder
Busk	Buskerud
Fnm	Finnmark
Hdm	Hedmark
Hrd	Hordaland
MöRo	Möre og Romsdal
Nrd	Nordland
NTrd	Nord-Tröndelag
Opl	Oppland
Östf	Östfold
Rog	Rogaland
SoFj	Sogn og Fjordane
STrd	Sör-Tröndelag
Tel	Telemark
Trs	Troms
VAgd	Vest-Agder
Vestf	Vestfold

Russian Fennoscandia:

Kk	Karelia keretina
Kol	Karelia olonetsensis
Kon	Karelia onegensis
Kpoc	Karelia pomorica occidentalis
Kpor	Karelia pomorica orientalis
Kton	Karelia transonegensis
Lim	Lapponia Imandrae
Lm	Lapponia murmanica
Lp	Lapponia ponojensis
Lt	Lapponia tulomensis
Lv	Lapponia Varsugae

Sweden:

Ång	Ångermanland
ÅsL	Lapponia åselensis (Åsele Lappmark)
Bh	Bohuslän
Bl	Blekinge
Dlr	Dalarne
Dls	Dalsland
Gbg	Göteborg region
Gstr	Gästrikland
Gtl	Gotland
Hl	Halland
Hls	Hälsingland
Hrj	Härjedalen
Jmt	Jämtland
Klm	Kalmar län (except Öl)
LL	Lapponia lulensis (Lule Lappmark)
LyL	Lapponia lyckselensis (Lycksele Lappmark)
Mpd	Medelpad
Nb	Norrbotten
Nrk	Närke
Ög	Östergötland
Öl	Öland
PL	Lapponia pitensis (Pite Lappmark)
Sk	Skåne (Scania)
Sm	Småland (except Klm)
Srm	Södermanland
TL	Lapponia tornensis (Torne Lappmark)
Upl	Uppland
Vb	Västerbotten
Vg	Västergötland
Vrm	Värmland
Vsm	Västmanland

The Danish provinces are subdivided into the districts of the Topographic – Botanical Investigation of Denmark (cf. e.g. Hylander 1966, p. 456), which are characterized by a "D" followed by a number.

Herbaria are abbreviated according to Lanjouw & Stafleu (1964). The collections from NMW are cited by a group of numerals from a current series by which the sheets of this herbarium are identified. All other sheets are cited as collector's name together with his own number or the collection year.

Numbers preceded by a "J" hint at the cultivated samples listed in App. 1.

Numbers in italics within brackets following the citations in App. 2–7 refer to figures (diagrams) for which the collections were employed.

The citations of Swedish, Norwegian and Finnish collections are generally initiated by the name of a town or a parish ("socken", "herred", "pitäjä").

APPENDICES

Appendix 1. List of spontaneous material kept in cultivation

The collection numbers refer to samples usually consisting of a number of plants from the same locality (cf. p. 14). Only the specific names stand for type subspecies or varieties. *R. islandica* is thus ssp. *islandica*, *R. palustris* is ssp. *palustris*, *R. curvipes* is var. *curvipes*. The abbreviations of countries and provinces are given in p. 167 f.. The localities are only briefly quoted. For a full account, see the labels of the voucher specimens preserved in UPS. For samples not collected by the author the sources (Botanical gardens, herbarium specimens, or field collectors) are given within brackets.

Collection number	Taxon	Chromosome number (2n)	Locality
J 136	*R. palustris*	32	Su. Srm, L. Malma, Eneboga, moist clayey soil
J 137	*R. palustris*	32	Su. Srm, Hyltinge, Långdunker, wet meadow
J 138	*R. palustris*	32	Su. Srm, Helgesta, Björnkärr, ditch
J 140	*R. palustris*	32	Su. Srm, Nyköping, Brandholmen, wet meadow
J 141	*R. palustris*	32	Su. Vb, Umeå, Grisbäcken, at a brook
J 142	*R. palustris*	32	Su. Ång, Näsåker, Nämforsen, river-shore among boulders
J 143	*R. sylvestris*	48	Su. Ång, Härnösand, Kanaludden, gravelly embankment
J 144	*R. palustris*	32	Su. Mpd, Sundsvall, R. Selångerån, river-shore
J 145	*R. palustris*	32	Su. Hls, Hudiksvall, at L. Lillfjärden
J 146	*R. palustris*	32	Su. Gstr, Gävle, Korsnäs, among boulders in a pier
J 147	*R. palustris*	32	Su. Srm, Ytterjärna, Yttre Eneby, ditch
J 169	*R. palustris*	32	Su. Hrj, Sveg, at R. Ljusnan close to the town
J 170	*R. palustris*	32	Su. Dlr, Mora, in the town at L. Siljan
J 171	*R. sylvestris*	48	Su. Srm, Oxelösund, Jogersö, garden
J 172	*R. palustris*	32	Su. Srm, Oxelösund, St. Vattungskäret, at a rock pool
J 174	*R. palustris*	32	Su. Srm, Oxelösund, Åkubben, at a rock pool
J 175	*R. palustris*	32	Su. Ög, Jonsberg, Penningskären, at a rock pool
J 176	*R. palustris*	32	Su. Klm, Halltorp, Värnaby, shore of a stream
J 177	*R. palustris*	32	Su. Bl, Bräkne-Hoby, at R. Bräkneån
J 178	*R. amphibia*	32	Su. Sk, Ivetofta, near Bromölla, at R. Skralbyån
J 179	*R. palustris*	32	Su. Sk, Kristianstad, in the town, at R. Helgeån
J 181	*R. palustris*	32	Su. Sk, Brönnestad, at L. Finjasjön, sandy shore
J 182	*R. palustris*	32	Su. Sm, Växjö, in the town, shore of L. Växjösjön
J 183	*R. palustris*	32	Su. Sm, Vetlanda, Kvarndammen, sandy shore

Collection number	Taxon	Chromosome number (2n)	Locality
J 184	*R. palustris*	32	Su. Ög, Svanshals, at R. Renstadsån near L. Tåkern
J 185	*R. sylvestris*	32	Su. Ög, Svanshals, at R. Renstadsån near L. Tåkern
J 186	*R. sylvestris*	32	Su. Vsm, Rytterne, Kvicksund, gravelly lake shore
J 187	*R. palustris*	32	Su. Upl, Svinnegarn, Fagerudd, sandy shore
J 188	*R. sylvestris*	48	Su. Nb, Luleå, in a park
J 189	*R. palustris*	32	Su. Dlr, Malung, at L. Bullsjön (I. & O. Hedberg)
J 190	*R. palustris*	32	Su. Nb, Luleå, in the town
J 192	*R. palustris*	32	Su. Upl, Harbo, Nybro, clayey soil at a stream
J 193	*R. palustris*	32	Su. Upl, Tensta, Skyttorp, at R. Fyrisån
J 252	*R. amphibia*	16	Ga. Spont. loc. (Bot. garden, Nantes)
J 253	*R. sylvestris*	48	Ga. Spont. loc. (Bot. garden, Nantes)
J 254	*R. palustris*	32	Su. Sk, Torekov, Hallands Väderö, Ulagapsviken (B. Lövkvist)
J 339	*R. amph.* × *sylv.*	32	Su. Srm, Sundby, Sundbyholm, sandy lake shore
J 340	*R. amphibia*	32	Su. Srm, Sundby, Sundbyholm, sandy lake shore
J 341	*R. amphibia*	32	Su. Srm, Strängnäs, Visholmen
J 342	*R. amphibia*	32	Su. Upl, Skokloster, near the castle
J 343	*R. palustris*	32	Su. Upl, Skokloster, near the castle, drift
J 344	*R. amph.* × *sylv.*	32	Su. Upl, Skokloster, near the castle
J 346	*R. amphibia*	32	Su. Upl, Skokloster, Norsholmen
J 347	*R. amph.* × *sylv.*	32	Su. Upl, Skokloster, Norsholmen, gravelly esker-shore
J 350	*R. palustris*	32	Su. Sk, Vomb, at L. Vombsjön, S.E. shore, on sand
J 351	*R. amphibia*	32	Su. Upl, Ekerö, Sandudden
J 353	*R. amphibia*	32	Su. Vsm, Rytterne, Tidö, on banks of drift
J 355	*R. amph.* × *sylv.*	32	Su. Upl, Övergran, Varpsund, gravelly esker-shore
J 356	*R. amph.* × *sylv.*	32	Su. Upl, Yttergran, Skälsund, gravelly esker-shore
J 357	*R. sylvestris*	40	Su. Upl, Uppsala, weed in the Botanic garden
J 358	*R. amphibia*	32	Su. Upl, Uppsala, at R. Fyrisån at Övre Föret
J 359	*R. palustris*	32	Su. Upl, Uppsala, at R. Fyrisån at Övre Föret
J 361	*R. sylvestris*	32	Su. Vsm, Badelunda, Björnön, Halsen, sandy esker-shore
J 364	*R. palustris*	32	Su. Vsm, Kungs-Barkarö, Malmön, gravelly esker-shore
J 366	*R. amphibia*	32	Su. Vsm, Kungs-Barkarö, Malmön, gravelly esker-shore
J 369	*R. palustris*	32	Su. Ög, Rystad, Ekängen, ditch
J 371, 372	*R. amph.* × *sylv.*	32	Su. Upl, Svinnegarn, Kolartorpet, sandy esker-shore
J 374	*R. palustris*	32	Su. Upl, Tierp, Sjölanda, at L. Tämnaren
J 375	*R. palustris*	32	Su. Upl, Tierp, Sjölanda, ditch
J 376	*R. amphibia*	32	Su. Upl, Tierp, Fors, at R. Tämnarån
J 377	*R. palustris*	32	Su. Upl, Hållnäs, Knöding, at R. Sladån
J 378	*R. amphibia*	32	Su. Upl, Forsmark, Johannisfors, at R. Forsmarksån
J 379	*R. amphibia*	32	Su. Upl, Börstil, Ledsundet, at the mouth of R. Olandsån

Collection number	Taxon	Chromosome number (2n)	Locality
J 380	*R. palustris*	32	Su. Upl, Börstil, Ledsundet, at the mouth of R. Olandsån
J 384	*R. amphibia*	32	Su. Upl, Uppsala, Lurbo, at R. Hågaån
J 385, 387	*R. amph.* × *sylv.*	32	Su. Upl, Uppsala, Lurbo, at R. Hågaån
J 390	*R. amphibia*	32	Su. Srm, Mariefred, Gripsholm
J 391	*R. palustris*	32	Su. Srm, Ytterselö, Stallarholmen
J 392	*R. amphibia*	32	Su. Srm, Ytterselö, Stallarholmen
J 393	*R. amphibia*	32	Su. Srm, Aspö, at the bridge to Oknö
J 394	*R. amph.* × *sylv.*	32	Su. Upl, Uppsala, at R. Hågaån S. of Lurbo
J 395	*R. amphibia*	32	Su. Upl, Uppsala-Näs, Vreta, at L. Ekoln (L. Junell)
J 398	*R. amphibia*	32	Su. Upl, Roslags-Bro, at L. Andersvedjaviken
J 399	*R. amphibia*	32	Su. Upl, Roslags-Bro, at R. Broströmmen near the church
J 400	*R. amphibia*	32	Su. Upl, Estuna, Norrmalma, at L. Erken
J 401	*R. sylvestris*	48	Su. Upl, Norrtälje, in the harbour
J 402	*R. palustris*	32	Fe. Ab, Mieitoinen, at R. Mynäjoki
J 403	*R. palustris*	32	Fe. Ab, Uusikaupunki, just E. of the town, at a pond
J 405	*R. palustris*	32	Fe. St, Pori, Rådmansholmen, at Kumo River
J 406	*R. amphibia*	32	Fe. St, Nakkila, at Kumo River near the highway bridge
J 408	*R. palustris*	32	Fe. St, Vammala, at Kumo River in the town
J 409	*R. amphibia*	32	Fe. Ta, Nokia, just E. of the town at L. Pyhäjärvi
J 410	*R. palustris*	32	Fe. Ta, Nokia, just E. of the town at L. Pyhäjärvi
J 411	*R. amphibia*	32	Fe. Ta, Lempäälä, at L. Toutosenselkä near the church
J 412	*R. amphibia*	32	Fe. Ta, Tyrväntö, at L. Vanajanselkä N. of the church
J 439	*R. sylvestris*	32	Fe. Nyl, Helsinge, S. of the church village, at Kervo River
J 440	*R. palustris*	32	Fe. Nyl, Helsinge, S. of the church village, at Kervo River
J 441	*R. sylvestris*	32	Fe. Nyl, Helsinge, near the church village, garden
J 442	*R. palustris*	32	Fe. Kb, Pielisjärvi, Paateri, at L. Jauhiainen
J 451	*R. palustris*	32	Fe. Kb, Pielisjärvi, Vuonisjärvi, Majalampi, road-bank
J 465	*R. palustris*	32	Fe. Ks, Kuusamo, Kokkoniemi, at L. Alakitka
J 466	*R. palustris*	32	Fe. Ob, Kemijärvi, in the town, at Kemi River
J 468	*R. palustris*	32	Fe. Ob, Kemijärvi, Vuostino, at a stream
J 471	*R. palustris*	32	Fe. Lk, Kittilä, at a stream N. of the church
J 472	*R. palustris*	32	Fe. Lk, Kittilä, Kaukonen, at R. Ounasjoki
J 473	*R. palustris*	32	Fe. Lk, Kittilä, Kallo, roadside
J 475	*R. palustris*	32	Fe. Lk, Muonio, Ylimuonio, road-bank
J 484	*R. palustris*	32	No. Trs, Målselv, at R. Målselven near the church

Collection number	Taxon	Chromosome number (2n)	Locality
J 486	*R. palustris*	32	No. Trs, Målselv, Moen, at R. Målselven
J 499	*R. palustris*	32	No. Fnm, Tana, Rustelfjelbma, at Tana River
J 504	*R. palustris*	32	No. Fnm, Tana, Tana bru, at Tana River
J 509	*R. palustris*	32	Fe. Li, Inari, church village, at L. Inari
J 510	*R. palustris*	32	Fe. Li, Inari, church village, at R. Vaskojoki
J 511	*R. palustris*	32	Fe. Li, Inari, Ivalo, at R. Ivalojoki
J 514	*R. palustris*	32	Fe. Lk, Sodankylä, church village, at R. Kitinen
J 515	*R. palustris*	32	Fe. Ob, Rovaniemi, Saarsenkylä, at a stream
J 516	*R. palustris*	32	Su. Nb, Haparanda, boat place at Torne River
J 518	*R. palustris*	32	Fe. Ob, Alatornio, Yliraumo, Keropudas, at a river-branch
J 519	*R. amphibia*	32	Fe. Ob, Alatornio, Yliraumo, Keropudas, at a river-branch
J 520	*R. amph.* × *sylv.*	32	Fe. Ob, Alatornio, Yliraumo, Keropudas, at a river-branch
J 524	*R. palustris*	32	Su. Upl, Estuna, at L. Norasjön (B. & C. Forsberg)
J 525	*R. palustris*	—	No. Nrd, Narvik, roadside (O. Hedberg)
J 526	*R. amph.* × *sylv.*	32	Su. Upl, Sigtuna, the bridge across L. Mälaren
J 528	*R. amphibia*	32	Su. Sk, Lackalänga, at R. Kävlingeån
J 529	*R. palustris*	32	Su. Upl, Skokloster, Norsholmen, gravelly shore
J 530	*R. amphibia*	32	Su. Upl, Sigtuna, at the bridge across L. Mälaren
J 531	*R. sylvestris*	48	Su. Upl, Uppsala, near the castle, nursery garden
J 532	*R. amph.* × *sylv.*	32	Su. Sk, Lackalänga, at R. Kävlingeån
J 533	*R. amphibia*	32	Su. Sk, Lomma, near the church, at R. Höjeån
J 534	*R. amph.* × *sylv.*	40	Su. Sk, Malmö, V. Skrävlinge, at the stream Risebergabäcken
J 535	*R. amph.* × *sylv.*	32	Su. Sk, Husie, Fridentorp, in a fen
J 536	*R. amph.* × *sylv.*	40	Su. Sk, Vomb, at L. Vombsjön, S.E. shore, on sand
J 537	*R. amphibia*	32	Su. Sk, Sövde, church village, at L. Sövdesjön
J 538	*R. amphibia*	32	Su. Sk, Husie, Fridentorp, in a fen
J 539	*R. sylvestris*	32	Su. Sk, Ignaberga, church village, fen in a pit
J 540	*R. austr.* × *sylv.*	32	Su. Sk, Stoby, Mostarna, bank at R. Skogbroån
J 541	*R. austr.* × *sylv.*	32	Su. Sk, Gumlösa, Fjärlöv, new bank at R. Fjärlövsån
J 542	*R. amphibia*	32	Su. Sk, Kristianstad, Långebro, at R. Helgeån
J 543	*R. amph.* × *sylv.*	32	Su. Sk, S. Åsum, at R. Tolångaån
J 544	*R. amphibia*	32	Su. Sk, Gårdstånga, Getinge, at R. Kävlingeån
J 548	*R. palustris*	32	Su. Gtl, Västergarn, at L. Paviken (B. Pettersson)
J 549	*R. amphibia*	32	Su. Upl, Övergran, Biskops-Arnö, at the bridge (B. & C. Forsberg)
J 550	*R. palustris*	32	Su. Gtl, Fårö, Kyrkviken, sandy beach at the sea (B. Pettersson)
J 573	*R. palustris*	32	Alaska. Arctic Coast Distr., Umiat, at Colville River (Mårtenssson No. U 19, UPS)
J 574	*R. barbareifolia*	16	Alaska. Bettles (E. Hultén)

Collection number	Taxon	Chromosome number (2n)	Locality
J 581	*R. sylvestris*	48	Su. Sk, Kristianstad, Långebro, bank at R. Helgeån
J 602	*R. sylvestris*	48	Su. Dlr, Leksand, church village, bank at L. Siljan (L. Junell)
J 619	*R. palustris*	32	Su. Ög, Kaga, at L. Roxen near the mouth of R. Svartån
J 620	*R. sylvestris*	32	Su. Ög, Kaga, at L. Roxen near the mouth of R. Svartån
J 621	*R. palustris*	32	Su. Ög, Källstad, Hånger, at L. Tåkern
J 672	*R. islandica*	16	Is. Árnessýsla, Birtingaholt
J 681	*R. islandica*	16	Is. Suður-Thingeyjarsýsla, Reykjahlíð, at L. Mývatn
J 721	*R. islandica*	16	Is. Suður-Thingeyjarsýsla, Neslönd, at L. Mývatn
J 778	*R. islandica*	—	Is. Suður-Thingeyjarsýsla, Geiteyjarströnd, at L. Mývatn
J 855	*R. palustris*	32	Su. Klm, Hallingeberg, Solhult (Nilsson No. 855, UPS)
J 856	*R. austr.* × *sylv.*	32	No. Akh, Oslo, T. Segerstedts Vei, nursery garden
J 858	*R. sylvestris*	32	No. Akh, Oslo, in the park at the Royal Castle
J 859	*R. sylvestris*	48	No. Östf, Moss, in the town, garden
J 860	*R. sylvestris*	48	No. Östf, Greåker, at a railway
J 864	*R. palustris*	32	Su. Sk, Holmby, Flyinge, at R. Kävlingeån
J 865	*R. sylvestris*	40	No. Akh, Oslo, weed in the Botanic garden
J 868	*R. austr.* × *sylv.*	32	Da. Sj, D 45b, Frederiksværk, in the town, dry courtyard
J 869	*R. sylvestris*	48	Da. Sj, D 45b, Frederikssund, Bilidt, roadside
J 870	*R. sylvestris*	32	Da. Sj, D 43, Fårevejle, near railway station
J 871	*R. amphibia*	32	Da. Sj, D 41, Sorö, in the town at the lake
J 872	*R. austr.* × *sylv.*	32	Da. Jl, D 25, Hejls (S.E. of Kolding), dry slope
J 873	*R. sylvestris*	32	Da. Jl, D 50, Hviding railway station
J 876	*R. palustris*	32	Da. Jl, D 25, Vejle, in the town, waste place
J 877	*R. sylvestris*	48	Da. Flst, D 37, Stubberup, garden
J 878	*R. sylvestris*	48	Da. Loll, D 35, Nakskov, in the harbour
J 879	*R. amphibia*	32	Da. Loll, D 35, Vesterborg, Hellinge Gård, at a stream
J 880	*R. amphibia*	32	Da. Loll, D 35, Sörup, at a pond
J 884	*R. amphibia*	32	Da. Loll, D 36, Maribo, at the lake in the town
J 885	*R. palustris*	32	Da. Sj, D 46, Köbenhavn, Islands Brygge, railway
J 886	*R. sylvestris*	48	Da. Sj, D 45a, Holte, garden
J 890	*R. sylvestris*	48	Su. Gbg, Göteborg, W. Cemetery
J 891	*R. sylvestris*	32	Su. Vsm, Västerås, in the town, near the mouth of R. Svartån
J 892	*R. sylvestris*	32	Su. Upl, Arnö, Oknö, Tjuvudden, esker-shore
J 899	*R. palustris*	32	Su. Gtl, Hörsne, Dibjers, bank at R. Dalhemsån
J 900	*R. sylvestris*	32	Su. Gtl, Hörsne, Dibjers, bank at R. Dalhemsån
J 912	*R. sylvestris*	48	Su. Gtl, Visby, Murfallet

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J 913	*R. sylvestris*	32	Su. Öl, Högsrum, Vedby, roadside
J 915	*R. palustris*	32	Su. Vsm, Lundby, Johannisberg, gravelly shore at L. Mälaren
J 916	*R. sylvestris*	32	Su. Vsm, Rytterne, N. of Mellansundet, esker-shore
J 917	*R. palustris*	32	Su. Srm, Torshälla, Torshälla huvud, esker-shore
J 918	*R. sylvestris*	32	Su. Srm, Vallby, Kullersta, Skomakarudden, esker-shore
J 919	*R. amphibia*	32	Su. Srm, Sundby, Sundbyholm, W. of the castle
J 920	*R. amph.* × *sylv.*	32	Su. Srm, Sundby, Sundbyholm, W. of the castle
J 921	*R. amph.* × *sylv.*	32	Su. Vsm, Rytterne, Kvicksund, esker-shore
J 922	*R. palustris*	32	Su. Upl, Dalby, Dalbyudd, gravelly shore
J 924	*R. amph.* × *sylv.*	32	Su. Upl, Dalby, Dalbyudd, gravelly shore
J 925	*R. amphibia*	32	Su. Upl, Dalby, Dalbyudd, gravelly shore
J 926	*R. amphibia*	32	Su. Upl, Solna, Huvudsta, at L. Ulvsundasjön
J 928	*R. palustris*	32	Su. Upl, Stockholm, Bromma, Traneberg, at L. Ulvsundasjön
J 929	*R. sylvestris*	32	Su. Upl, Munsö, Österås, esker-shore
J 930	*R. amphibia*	32	Su. Upl, Munsö, Österås, esker-shore
J 931	*R. amphibia*	32	Su. Upl, Hilleshög, Hillersjö, at L. Mälaren
J 932	*R. amphibia*	32	Su. Upl, Hilleshög, between Norrudden and Margithill, at L. Mälaren
J 933–935	*R. amph.* × *sylv.*	32	Su. Upl, Skokloster, Arnöhuvud, esker-shore
J 936	*R. amph.* × *sylv.*	32	Su. Upl, Häggeby, Eknäs, Sandreveln, esker-shore
J 937	*R. amphibia*	32	Su. Upl, Häggeby, Eknäs, Sandreveln, esker-shore
J 938	*R. palustris*	32	Su. Nb, Tärendö, church village, meadow at Kalix River (Alm No. 3860, UPS)
J 939	*R. palustris*	32	No. Hrd, Fana, Flessland, roadside (1960 Naustdal, BG)
J 940	*R. palustris*	32	No. Hrd, Modalen, Otterstad, gravelpit (1958 Langedal, BG)
J 941	*R. palustris*	32	No. Hrd, Bruvik, Vaksdal Mill (Ouren No. 21530, BG)
J 942	*R. palustris*	32	Su. Nb, Tärendö, Saittajärvi, at the lake (Alm No. 3730, UPS)
J 943	*R. palustris*	32	U.S.S.R. Latvia, Salaspils (Bot. gard., Acad. Sci. Latv.)
J 944	*R. islandica*	16	Br. Scotland, Midlothian, Pentland Hills, Threipmuir Reservoir, marshes (Currie, Edinb. No. 0717, E)
J 946	*R. palustris*	32	Su. Vsm, Möklinta, near Tyttboforsen, at R. Dalälven
J 949	*R. palustris*	32	Su. Hls, Söderhamn, waste place (Lundqvist No. 3670, UPS)
J 950	*R. palustris*	32	No. Hrd, Fana, between Nesttun and Hop bru, road (1959 Naustdal, BG)
J 952	*R. amphibia*	16	Lu. Spont. loc. (Bot. gard., Coimbra)

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J 954	*R. palustris*	32	Cz. E. Slovakia, Královský Chlemec (Bot. gard., Bratislava)
J 955	*R. amphibia*	16	Br. England, Oxfordshire, Goring, at R. Thames (I. & O. Hedberg)
J 957	*R. palustris*	32	Ga. Cantal, St. Flour, alt. 750 m (Bot. gard., Toulouse)
J 958	*R. sylvestris*	32	Hu. Spont. loc. (Bot. gard., Inst. pl. med., Budapest)
J 959	*R. palustris*	32	Fe. Ob, Kempele, Roivinen (1961 Jokela, S)
J 960	*R. sylvestris*	48	Su. Upl, Vaksala, Fridhem, waste place (N. Lundqvist)
J 961	*R. amphibia*	32	Su. Vsm, Rytterne, Tidö-Lindö (I. Nordin)
J 962	*R. sylvestris*	32	Lu. Spont. loc. (Bot. gard., Coimbra)
J 963	*R. sylvestris*	48	Su. Bh, Resteröd, Ranneberg, garden
J 964	*R. palustris*	32	Su. Bh, Svarteborg, Hede, at L. S. Bullaren
J 965	*R. palustris*	32	No. Östf, Idd, 2 km S of the church, ditch
J 977	*R. islandica*	16	No. Nrd, Væröy, W. of Nordland village
J 1046	*R. islandica*	16	No. Nrd, Nordvik, Vandve, near Vandve gård
J 1055	*R. islandica*	16	No. Nrd, Dönnes, Åsvær, Risöy
J 1058	*R. islandica*	16	No. Nrd, Dönnes, Åsvær, Buröy
J 1068	*R. sylvestris*	48	No. STrd, Trondheim, Singsaker, square garden
J 1069	*R. sylvestris*	48	No. Akh, Oslo, weed in the Botanic garden
J 1070	*R. sylvestris*	48	No. Akh, Oslo, Trondheimsveien, square garden
J 1071	*R. palustris*	32	Su. Vrm, Karlstad, near the hospital at R. Klarälven
J 1073	*R. palustris*	32	Ga. Spont. loc. (Bot. gard., Dijon)
J 1074	*R. sylvestris*	32 (37)	Ga. Spont. loc. (Bot. gard., Dijon)
J 1075	*R. palustris*	32	U.S.S.R. Armenia, spont. loc. (Bot. gard., Erevan)
J 1076	*R. sylvestris*	32	Su. Hls, Ljusdal, Lillhaga, at L. Borrsjön
J 1077	*R. palustris*	32	Su. Hls, Ljusdal, Lillhaga, at L. Borrsjön
J 1078	*R. palustris*	32	Su. Hls, Bollnäs, in the town, at R. Ljusnan
J 1079	*R. palustris*	32	Su. Gstr, Hedesunda, Ön, at R. Dalälven, esker-shore
J 1080	*R. palustris*	32	Su. Jmt, Åre, Storlien, railway station (L. Junell)
J 1081	*R. palustris*	32	Su. Vb, Degerfors, Ottonträsk, at the bridge across Ume River (I. & O. Hedberg)
J 1082	*R. sylvestris*	48	Su. Upl, Stockholm, Bromma, Abrahamsberg (S. Nilsson)
J 1083	*R. sylvestris*	48	Su. Upl, Solna, Huvudsta, Nybodagatan (S. Nilsson)
J 1084	*R. palustris*	32	Su. Öl, Gårdby, Gårdby harbour, on drift of seaweed
J 1085	*R. amph.* × *sylv.*	40	Su. Sk, Kristianstad, in the town, at the E. Canal
J 1088	*R. amphibia*	32	Su. Sk, Kristianstad, in the town, at the E. Canal
J 1089	*R. palustris*	32	Su. Sk, Eljaröd, Gumhusa, at pool
J 1090	*R. austr.* × *sylv.*	32	Su. Sk, Eljaröd, Tjörneröds mölla, dry roadside
J 1091	*R. amph.* × *sylv.*	40	Su. Sk, Öved, at L. Vombsjön, E. shore, on sand
J 1092	*R. amphibia*	32	Su. Sk, Öved, at L. Vombsjön, E. shore, on sand

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J 1093	*R. palustris*	32	Su. Sk, Öved, at L. Vombsjön, E. shore, on sand
J 1095	*R. amph.* × *sylv.*	32	Su. Sk, Harlösa, N.W. shore of L. Vombsjön
J 1096	*R. amphibia*	32	Su. Sk, Harlösa, N.W. shore of L. Vombsjön
J 1099	*R. amphibia*	32	Su. Sk, Vomb, W. shore of L. Vombsjön
J 1100	*R. amphibia*	32	Su. Sk, Silvåkra, at L. Krankesjön
J 1102	*R. palustris*	32	Su. Sk, Falsterbo, Flommen
J 1103	*R. sylvestris*	48	Su. Sk, Landskrona, in the town, garden
J 1104	*R. amphibia*	32	Su. Sk, V. Sönnarslöv, Klippans Bruk, at the Rönne River
J 1105	*R. palustris*	—	Su. Sk, V. Sönnarslöv, Klippans Bruk, at the Rönne River
J 1107	*R. palustris*	32	Su. Sk, Osby, at N. end of L. Osbysjön
J 1108	*R. sylvestris*	48	Su. Sk, Höganäs, in the town, waste place
J 1109	*R. sylvestris*	48	Su. Hl, Laholm, Altona, roadside
J 1112	*R. amphibia*	32	Su. Upl, Knutby, S. of Vällnora, at L. Norrsjön
J 1113	*R. sylvestris*	48	Fe. Nyl, Helsingfors, Sandudd, cemetery
J 1114	*R. austr.* × *sylv.*(?)	32	Fe. Nyl, Helsingfors, Hesperia Park, near L. Tölöviken
J 1116	*R. sylvestris*	32	Ju. Istria, Rovinj, roadside (U. Starbäck)
J 1117	*R. palustris*	32	Su. Hls, Ytterhogdal, at L. Kyrksjön (Nannfeldt No. 18082, UPS)
J 1118	*R. palustris*	32	Fe. Le, Enontekiö, Palojoensuu (Ahti No. 1301, H)
J 1119	*R. palustris*	32	Fe. St, Merikarvia, Lautjärvi, Vähäjärvi (1962 Suominen, H)
J 1120	*R. palustris*	32	Fe. Le, Enontekiö, Kilpisjärvi (1961 Roivainen, H)
J 1123	*R. austriaca*	16	Ga. Côte-d'Or, Longvic (Bot. gard., Dijon)
J 1126	*R. palustris*	32	Fe. St, Merikarvia, harbour (1962 Suominen, H)
J 1127	*R. sylvestris*	32	Lu. Spont. loc. (Bot. gard., Coimbra)
J 1128	*R. curvipes*	16	Canada. Saskatchewan, Creelman (Alex & Gebhardt No. 1205, DAO)
J 1129	*R. sylvestris*	32	Hu. Spont. loc. (Bot. gard., Budapest)
J 1130	*R. palustris*	32	Su. Sk, V. Vram, Tollarp (Bot. gard., Lund)
J 1132	*R. palustris*	32	Su. Sk, Barsebäck (Bot. gard., Lund)
J 1133	*R. palustris*	32	Fe. Kb, Kuusjärvi, Harmaasalo (Bot. gard., Helsingfors)
J 1134	*R. palustris*	32	Ge. Spont. loc. (Bot. gard., Marburg)
J 1135	*R. sylvestris*	32 (33)	Ga. Nièvre, La Charité-sur-Loire (Bot. gard., Lab. pl. fourragères, Rouen)
J 1136	*R. palustris*	32	Ga. Bas-Rhin, Eschau, Plobsheim (Bot. gard., Strasbourg)
J 1137	*R. palustris* ssp. *fernaldiana*	32	U.S.A. Wisconsin, Duluth Superior Harbour, Bakers Island (Monson No. 4077, DUL)
J 1139	*R. palustris*	32	Su. Dlr, Ludvika (G. Eriksson)
J 1140	*R. amphibia*	32	Ge. Niedersachsen, Lingen, at R. Ems

Collection number	Taxon	Chromosome number (2n)	Locality
J 1142	*R. amphibia*	32	Ho. Gelderland, Zutphen, at pond in the town
J 1145	*R. palustris*	32	Ho. Brabant, St. Oedenrode
J 1146	*R. amphibia*	32	Be. Antwerpen distr., Herenhals, at the river
J 1147	*R. amphibia*	16	Be. Antwerpen distr., Liezele, ditch
J 1148	*R. amph.* × *sylv.*	40	Br. England, W. Sussex, Houghton, at R. Arun
J 1149	*R. amphibia*	32	Br. England, W. Sussex, Houghton, at R. Arun
J 1150	*R. amph.* × *sylv.*	32	Br. England, W. Sussex, Houghton, at R. Arun
J 1151	*R. palustris*	32	Br. England, W. Sussex, Houghton, at R. Arun
J 1152	*R. amphibia*	32	Br. England, W. Sussex, Pulborough, Swan Bridge, at R. Arun
J 1159	*R. amphibia*	16	Br. England, Berkshire, Henley, at R. Thames
J 1160	*R. amphibia*	16	Br. England, Oxfordshire, Shiplake, at R. Thames
J 1161	*R. amphibia*	16	Br. England, Berkshire, Pangbourne, at R. Thames
J 1165	*R. sylvestris*	48	Br. England, Oxfordshire, Shiplake, at R. Thames
J 1166	*R. amphibia*	16	Br. England, Wiltshire, Lechlade, at R. Thames
J 1167	*R. amph.* × *pal.*	32	Br. England, Gloucestershire, Tewkesbury, ditch
J 1168, 1169	*R. amph.* × *sylv.*	32	Br. England, Gloucestershire, Tewkesbury, at R. Avon
J 1170	*R. amph.* × *sylv.*	32	Br. England, Worcestershire, Worcester, at R. Severn
J 1171, 1172	*R. amph.* × *sylv.*	32	Br. England, Worcestershire, Bewdley, at R. Severn
J 1175	*R. amphibia*	32	Hb. N. Ireland, Armagh, Charlestown, at Lough Neagh
J 1176	*R. palustris*	32	Hb. N. Ireland, Armagh, Charlestown, at Lough Neagh
J 1177	*R. palustris*	32	Hb. N. Ireland, Armagh, 5 km N. of Portadown, at R. Bann
J 1188	*R. amphibia*	32	Hb. Eire, Roscommon, Ballyclare, at L. Ree
J 1212	*R. islandica*	16	Hb. Eire, W. Galway, Connemara, Renvyle
J 1220	*R. austr.* × *sylv.*	32	No. Akh, Oslo, the park at the Royal Castle
J 1221	*R. sylvestris*	32	No. Akh, Oslo, Bygdöy, near the S.E. point, gravelly shore
J 1222	*R. amph.* × *sylv.*	32	Su. Srm, Strängnäs, Ulfhäll, at L. Mälaren
J 1223	*R. amphibia*	32	Su. Upl, Edsbro, at road bank across L. Närdingen
J 1224	*R. amph.* × *sylv.*	32	Su. Upl, Dalby, W. of Vreta udd, at L. Mälaren
J 1225	*R. palustris*	32	U.S.S.R. N.E. Russia (Bot. gard., Leningrad)
J 1234	*R. sylvestris*	48	Su. Klm, Ryssby, Rockneby, sandy roadside
J 1235	*R. sylvestris*	48	Su. Sk, Öved, E. shore of L. Vombsjön, on sand
J 1236, 1237	*R. amph.* × *sylv.*	40	Su. Sk, Öved, E. shore of L. Vombsjön, on sand
J 1238–1240	*R. amphibia*	32	Su. Sk, Öved, E. shore of L. Vombsjön, on sand
J 1241	*R. amphibia*	c. 32	Su. Sk, Benestad, at R. Fyleån
J 1242	*R. palustris*	c. 32	Su. Sk, Benestad, at R. Fyleån
J 1243	*R. sylvestris*	c. 48	Su. Upl, Stockholm, Frescati, square garden
J 1244–1251	*R. amph.* × *sylv.*	32	Su. Upl, Skokloster, Arnöhuvud, E. side, at L. Mälaren
J 1252	*R. amphibia*	32	Su. Upl, Sigtuna, N. of the bridge across L. Mälaren

Collection number	Taxon	Chromosome number (2n)	Locality
J 1253	*R. amph.* × *sylv.*	—	Su. Upl, Sigtuna, in the town at L. Mälaren
J 1254	*R. sylvestris*	48	Su. Upl, Uppsala, Luthagen, lawn
J 1260	*R. amph.* × *sylv.*	32	Su. Srm, Sundby, Sundbyholm
J 1262	*R. amph.* × *sylv.*	—	Su. Vsm, Rytterne, Kvicksund, esker-shore
J 1263	*R. palustris*	—	Su. Vsm, Rytterne, Kvicksund, esker-shore
J 1264	*R. palustris*	—	Su. Upl, Uppsala, Lurbo, at R. Hågaån
J 1267	*R. palustris*	32	Su. Upl, Alsike, between Kungshamn and Fredrikslund, at L. Mälaren
J 1270	*R. palustris*	—	Su. Upl, Edsbro, on road bank across L. Närdingen
J 1271	*R. amphibia*	16	Br. England, Surrey, Kew, at R. Thames
J 1278	*R. pyrenaica*	16	Ga. Haute-Garonne, Vallée de Lys (Bot. gard., Leicester)
J 1279	*R. palustris*	—	Su. Upl, Uppsala-Näs, N. of Vreta udd, at L. Mälaren
J 1280	*R. palustris*	32	U.S.S.R. Leningrad distr. (Bot. gard., Leningrad)
J 1281	*R. curvisiliqua*	16	U.S.A. California, Plumas Co., at Feather River (Mosquin & Gillett No. 5303, DAO)
J 1282	*R. palustris* ssp. *fernaldiana*	32	Canada. Alberta, at Elkwater Lake (Mosquin & Benn No. 4716, DAO)
J 1285	*R. palustris* ssp. *fernaldiana*	32	Canada. Quebec, Stanstead Co., at L. Memphremagog (Mosquin & Spicer No. 6378, DAO)
J 1286	*R. curvipes*	16	U.S.A. Wyoming, Carbon Co., Riverside (Mosquin & Gillett No. 5340, DAO)
J 1288	*R. curvipes*	16	Canada. Brit. Columbia, Queen Charlotte Isl., Graham I., Tlell (Calder & Taylor No. 36876, DAO)
J 1289	*R. curvipes*	16	U.S.A. Colorado, Custer Co., Sangre de Cristo Mts (Mosquin & Gillett No. 5382, DAO)
J 1290	*R. pyrenaica*	16	Rm. Spont. loc. (Bot. gard., Cluj)
J 1294	*R. palustris*	32	Br. Scotland, Midlothian, Borthwick (Collum-Webster No. 8753, CGE)
J 1295	*R. pyrenaica*	16	Ga. E. Pyrenees (Bot. gard., Techn. Univ. Dresden)
J 1297	*R. palustris*	32	Ga. Côte-d'Or, Grosbois-en-Montagne (Bot. gard., Dijon)
J 1298	*R. palustris*	32	Ge. Niedersachsen, R. Leda (Bot. gard., Oldenburg)
J 1299	*R. palustris*	c. 32	Fe. Ob, Oulu (Bot. gard., Oulu)
J 1300	*R. palustris*	32	Fe. Sa, Imatra (Bot. gard., Helsingfors)
J 1301	*R. palustris*	32	Fe. Sa, Punkaharju (Bot. gard., Helsingfors)
J 1302	*R. palustris*	32	Fe. Ta, Ylöjärvi (Bot. gard., Helsingfors)
J 1303	*R. palustris*	32	Fe. Ta, Tampere (Bot. gard., Helsingfors)
J 1304	*R. palustris*	32	Fe. Nyl, Strömfors (Bot. gard., Helsingfors)
J 1305	*R. palustris*	32	Fe. Sb, Varkaus (Bot. gard., Helsingfors)
J 1307	*R. sylvestris*	48	Su. Sk, Öved, E. shore of L. Vombsjön
J 1311	*R. amph.* × *sylv.*	40	Su. Sk, Öved, E. shore of L. Vombsjön
J 1312	*R. amph.* × *sylv.*	40	Su. Sk, Fränninge, near the church, at R. Fränningeån

Collection number	Taxon	Chromosome number (2n)	Locality
J 1314	*R. amph.* × *sylv.*	32	Su. Sk, Fränninge, near the church, at R. Fränningeån
J 1320	*R. amphibia*	16	Ga. Spont. loc. (Bot. gard., Besançon)
J 1321	*R. amphibia*	32	Su. Upl, Funbo, Korsbacken, at L. Ramsen
J 1382	*R. amphibia*	32	Su. Upl, Kungs-Husby, at the bridge leading to Grönsöö
J 1383	*R. amphibia*	32	Su. Upl, Låssa, Björknäs, Kvistabergsviken
J 1384	*R. sylvestris*	32	Ju. Serbia, S. of Titovo Užice, Zlatibor (B. Pettersson)
J 1385	*R. amphibia*	32	Su. Srm, Överselö, Ekebyvik, Algöviken
J 1386	*R. amphibia*	—	Su. Srm, Överselö, N. of Kråkudden, opposite Lindön
J 1387	*R. palustris*	32	Su. Srm, Helgarö, Helgaröklapp, esker-shore
J 1388	*R. sylvestris*	32	Su. Srm, Helgarö, Helgaröklapp, esker-shore
J 1389	*R. palustris*	32	Su. Srm, Aspö, Näsudden
J 1390	*R. amphibia*	32	Su. Srm, Aspö, Sanda, opposite Sanda holme
J 1391	*R. amphibia*	32	Su. Upl, Skokloster, 300 m E. of Norsholmen
J 1394	*R. palustris*	32	Su. Upl, Skokloster, 300 m E. of Norsholmen
J 1395	*R. amphibia*	32	Su. Upl, Adelsö, Hanholmen
J 1396	*R. amphibia*	32	Su. Upl, Adelsö, Rörviken
J 1397	*R. amphibia*	32	Su. Upl, Adelsö, 500 m E. of the church
J 1432	*R. amphibia*	32	Su. Upl, Munsö, Svinsundet, Sjöängen
J 1440	*R. palustris*	32	Fe. Om, Gamlakarleby, Yxpila (Bot. gard., Åbo)
J 1441	*R. palustris*	32	Da. Jl, D 21, Århus (1962 Lütken, C)
J 1447	*R. palustris*	32	Canada. Quebec, Papineaulo, Thurso, at Ottawa R. (Dore No. 20142, DAO)
J 1449	*R. palustris*	32	Da. Sj, D 45a, Herlev Station (1961 A. Hansen, C)
J 1452	*R. palustris*	32	Canada. Mackenzie Distr., Snowdrift, E. end of Great Slave Lake (Cody No. 14713, DAO)
J 1453	*R. palustris*	32	Canada. Mackenzie Distr., Tsu Lake (Cody No. 14213, DAO)
J 1455	*R. palustris*	32	Au. Steiermark, Edlach at Trieben (Bot. gard., Graz)
J 1456	*R. palustris*	32	Su. Ång, Gudmundrå, at L. Nattsjön, embankment (Lundqvist No. 4011, UPS)
J 1457	*R. palustris*	c. 32	Fe. Sa, Rantasalmi (Bot. gard., Helsingfors)
J 1458	*R. palustris*	32	Fe. Tb, Jyväskylä (Bot. gard., Helsingfors)
J 1459	*R. palustris*	32	Fe. Kb, Kontiolahti (Bot. gard., Helsingfors)
J 1461	*R. palustris*	32	Ge. Hessen, Nidda (Bot. gard., Marburg)
J 1462	*R. amphibia*	16	Ge. Hessen, Erfelden (Bot. gard., Marburg)
J 1463	*R. sylvestris*	32	Lu. Spont. loc. (Bot. gard., Coimbra)
J 1465	*R. sylvestris*	32	Hu. Spont. loc. (Bot. gard., Inst. pl. med., Budapest)
J 1467	*R. palustris*	32	Po. Silesia (Hort. plant. medic., Wrocław)
J 1468	*R. palustris*	32	Ge. Oldenburg (Bot. gard., Oldenburg)
J 1469	*R. palustris*	32	Fe. Lk, Kittilä (Bot. gard., Oulu)
J 1470	*R. palustris*	32	Cz. Bohemia, Protivin (Bot. gard., Průhonice)
J 1472	*R. palustris*	32	Canada. Saskatchewan, Whitewood (Alex & Gebhardt No. 1233, DAO)

Collection number	Taxon	Chromosome number (2n)	Locality
J 1473	*R. palustris*	32	Canada. Saskatchewan, Regina (Alex No. 1058, DAO)
J 1476	*R. curvipes*	16	Canada. Saskatchewan, Pangman (Alex No. 1169, DAO)
J 1477	*R. palustris*	32	Canada. Saskatchewan, Estlin (Alex & Gebhardt No. 1485, DAO)
J 1479	*R. sessiliflora*	16	U.S.A. Arkansas, Clark Co., Arkadelphia (Bassett & Spicer No. 04513, DAO)
J 1480	*R. amphibia*	32	Su. Upl, Knutby, at L. Kärven
J 1481	*R. palustris*	32	Fe. Ob, Kuivaniemi, at L. Oijärvi (1963 Jokela, UPS)
J 1504	*R. palustris*	32	Su. Vg, Sävare, Truve, at L. Vänern
J 1507	*R. palustris*	32	Su. Vg, Skara, in the town, ditch
J 1517	*R. palustris*	32	Su. Bh, Tanum, near the railway station, ditch
J 1522	*R. palustris*	32	Su. Nrk, Tysslinge, ditch S. of L. Tysslingen
J 1526	*R. amphibia*	—	Su. Upl, Dalby, W. of Vreta udd, at L. Mälaren
J 1539	*R. palustris*	32	U.S.S.R. Kazakhstan, Pavlodarskaya obl., Belovodskaya, at R. Irtysh (Bot. gard., Alma-Ata)
J 1541	*R. amph.* × *sylv.*	32	Su. Upl, Skokloster, Norsholmen, N.E. shore on gravel
J 1542	*R. amph.* × *sylv.*	32	Su. Upl, Skokloster, Bagarbo, at L. Mälaren, sandy shore
J 1544	*R. amphibia*	32	Da. Sj, D 46, Köbenhavn, Utterslev Mose
J 1545	*R. sylvestris*	48	Da. Sj, D 45a, Gentofte, Nygårdsvej, waste place
J 1547	*R. palustris*	32	Da. Sj, D 45b, Nödebo, at S. end of Esrum Lake
J 1548	*R. amphibia*	32	Da. Sj, D 45b, Huseby, (S. of Ramlöse), at L. Arresö
J 1549, 1550	*R. palustris*	32	Da. Sj, D 45b, Annisse, E. side of L. Arresö, at a stream
J 1551	*R. amphibia*	32	Da. Sj, D 45b, Annisse, E. of side L. Arresö, at a stream
J 1552	*R. austriaca*	16	Da. Jl, D 27, N. Nebel, at a railway
J 1553	*R. amphibia*	32	Da. Jl, D 26, Varde, in the town, at Varde River
J 1554	*R. palustris*	32	Da. Jl, D 26, Varde, in the town, at Varde River
J 1555	*R. amphibia*	c. 32	Da. Jl, D 27, Ribe, Kurveholmen, at Ribe River
J 1556	*R. amphibia*	32	Da. Jl, D 27, Ribe, Ribershus, at the fosse
J 1557	*R. palustris*	32	Da. Jl, D 27, Ribe Ribershus, close to Ribe River
J 1558	*R. palustris*	32	Da. Jl, D 49, Foldingbro, at Konge River
J 1559	*R. amphibia*	c. 32	Da. Jl, D 25, Harte (W. of Kolding), church village at a pond
J 1560	*R. palustris*	32	Da. Jl, D 25, Harte (W. of Kolding), church village, at a pond
J 1561	*R. amphibia*	32	Da. Fyn, D 28, Glamsbjerg, at a lake E. of the village
J 1562	*R. amphibia*	32	Da. Fyn, D 32, S. Broby, in the village, at a stream

Collection number	Taxon	Chromosome number (2n)	Locality
J 1563	*R. palustris*	32	Da. Sj, D 42, Sæby, near the church, at L. Tissö
J 1566	*R. palustris*	32	He. Graubünden, Silsersee near St. Moritz, c. 1800 m (I. & O. Hedberg)
J 1567	*R. sylvestris*	48	Ho. Gelderland, Lelystad (I. & O. Hedberg)
J 1568	*R. palustris*	32	Br. England, Essex, Hutton near Brentwood (R. Ellis)
J 1569	*R. palustris*	32	Su. Hl, Älvsåker, Alafors (1964 Ohlander, GB)
J 1570	*R. palustris*	32	Su. Hl, Lindome, between Sagsjön and Långeslätt (1963 Ohlander, GB)
J 1571	*R. palustris*	32	Su. Hl, Lindome, Anderstorp (1963 Ohlander, GB)
J 1572	*R. palustris*	32	Su. TL, Karesuando, church village (O. Hedberg)
J 1573	*R. palustris*	32	Alaska. Lower Yukon R., Holycross (1965 Hultén, S)
J 1574	*R. palustris*	32	Alaska. Lower Yukon R., Ilivit Mts (1965 Hultén, S)
J 1575	*R. palustris*	32	Alaska. Kotzebue (1964 Hultén, S)
J 1576	*R. palustris*	32	Alaska. Lower Yukon R., Marshall, Mt Okumiak (1965 Hultén, S)
J 1577	*R. sylvestris*	32	Rm. Spont. loc. (Bot. gard., Univ. Bucureşti)
J 1580	*R. amphibia*	16	Ga. Meurthe-et-Moselle, La Neuveville de Nancy (Bot. gard., Nancy)
J 1585	*R. palustris*	32	No. Hrd, Bergen, Hatleberg (Bot. gard., Bergen)
J 1586	*R. palustris*	32	Ge. Hessen, Kr. Büdingen, Engelrod (Bot. gard., Marburg)
J 1587	*R. sylvestris*	32 (31)	Ga. Seine maritime, Duclair (Bot. gard., Lab. pl. fourragères, Rouen)
J 1590	*R. icarica*	16	Turkey. Ikaria, Mt. Atheras (Runemark & Snogerup No. 12441, LD)
J 1591	*R. palustris*	32	Ge. Brandenburg, Zehdenick (Bot. gard., Halle)
J 1593	*R. sylvestris*	—	Su. Vb, Umeå, University area, garden

Appendix 2. Collections of *Rorippa islandica*

Cited within brackets are literature records not verified by herbarium material. For further explanations see p. 167.

R. islandica ssp. *islandica*

NORWAY

Nordland: Væröy, Nordland village, 1898, J. R. LANDMARK (BG) and 1963, J 977 (*2*, *4*). Dönnes, Åsvær, Buröy, 1910, O. DAHL (O) and 1963, J 1058 (*1*, *2*, *3*, *4*), Risöy, 1963, J 1055 (*2*, *4*). Nordvik, Vandve, 1910, O. DAHL (O) and 1963, J 1046 (*1*, *2*, *3*, *4*).

ICELAND

Rangárvallsýsla: Eyvindarhólar, 1901, H. JÓNSSON (C, ICEL). *Árnessýsla:* Urridafoss, 1911, H. JÓNSSON (ICEL). Syðri Reykir, 1895, M. HELGASON (ICEL). Húsalóftir, 1917, H. JÓNSSON (ICEL). Skeið, S. of Vörðufell, 1928, SÖRENSEN (C). Birtingaholt, 1917, H. JÓNSSON (C) and J 672 (*2*, *4*). Biskupstungur, Torfustaðir, 1895, M. HELGASON (ICEL, *1*); Efri-Reykir, 1889, Anon. (C, *4*). Laugarvatnsvellir, 1911, H. JÓNSSON (C, ICEL). *Gullbringusýsla:* Kaldárseli, Helgadalur, 1945, F. GUÐMUNDSSON (ICEL). *Snæfellsnessýsla:* Hagavatn, 1897, H. JÓNSSON (C, ICEL). *Eyjafjarðarsýsla:* Litliárskógssandur, 1899, S. STEFÁNSSON (ICEL) and Ó. DAVÍÐSSON (C, ICEL, *1*, *2*, *3*, *4*). Árskógutrönd, Móatjörn, 1935, I. DAVÍÐSSON (ICEL). Hella, 1931, I. DAVÍÐSSON (C, *1*, *2*, *3*, *4*). Hrísey, 1926, I. ÓSKARSSON (ICEL). *Suður-Thingeyjarsýsla:* Vaglar, Fnjóskadalur, 1891, S. STEFÁNSSON (BM, C, ICEL, *1*, *2*, *3*, *4*). Laxá, Brúarfoss, 1884, PEDDERSEN (C, *1*, *2*, *3*, *4*). Mývatnssveit at L. Mývatn, 1876, C. GRÖNLUND (C, UPS, *1*, *4*), 1931, MEINERTZHAGEN & CLAY No. 886 (BM) and 1941, CANDWELL No. 87 (K), S. shore, 1935, V. ROMOSE (C), Skútustaðir, 1933, T. SÖRENSEN (C, UPS), 1935, I. DAVIÐSSON (C) and J. GRÖNTVED (C), 1941, F. GUÐMUNDSSON (ICEL), Geiteyjarströnd, 1935, V. ROMOSE (C) and J 778, Vogar, J 766, Reykjahlíð, 1876 and 1884, THORODDSEN (C, UPS), 1876, C. GRÖNLUND (C), 1934, A. JÖRGENSEN (C) and J 681 (*2*), Neslönd, J 721 (*1*, *2*, *3*, *4*), Grímstaðir, J. JÓNSSON (ICEL). Mývatnssveit, Grænavatn, 1894 (*1*, *2*, *3*, *4*), and Stóragjá, 1895, S. STEFÁNSSON (C, ICEL), Laxamýri, 1898, J. SIGURJÓNSSON (ICEL). Grímsey, 1898, Ó. DAVÍÐSSON (C, ICEL *1*, *2*, *3*, *4*). *Norður-Thingeyjarsýsla:* Kelduhverfi, Ásbyrgi, 1895, S. STEFÁNSSON (C, ICEL); Víkingavatn, 1895, S. STEFÁNSSON (C, ICEL).—Without locality: 1772, BANKS & SOLANDER (BM). 1876, W. L. LINDSAY (K).

GREAT BRITAIN

Orkney Islands: N. Ronaldsey, Loch of Garsow, 1908, M. SPENCE (E) and 1920, H. H. JOHNSTON (BM, E, K, *2*, *4*); Loch of Hooking, 1920, H. H. JOHNSTON (E). *Midlothian:* Pentland Hills, Threipmuir Reservoir, 1956, CURRIE, E No. 0717 (E, UPS) = J 944 (*1*, *2*, *3*, *4*). *Wigtown:* near Sandhead, 1934, G. TAYLOR (BM, *1*, *2*, *3*, *4*). *Isle of Man:* Andreas, in dried up pond towards Smeale, 1933, C. I. PATON (BM, *1*, *4*).

IRELAND

W. Galway: Connemara, Renvyle, 1831 and 1832, herb. SHUTTLEWORTH (BM, DBN) and 1964, J 1212 (*1*, *2*, *3*, *4*).

FRANCE

Ariège: Couflens, 1800 m, pasture, 1927, Anon. (TL). *Haute-Garonne:* St. Béat, moist places, 1872, BORDÈRE (K, *1*, *4*). *Alpes maritimes:* Bergerie de Sanguinière (near the sources of R.

Var), marsh, 1877, E. Burnat (W). *Hautes-Alpes:* [Mt. Gondran (near Briançon), Villars (1789)]. *Savoie:* Mt. Cenis, 1828, A. Lyon (C) and near the small lake, E. Bourgeau (K, *1*, *4*). L. Mt. Cenis, 1863, B. Verlot (P); dried out pool, 1863, E. Perrier (G). Mt. Cenis, 1878 E. A. Willmott (K, *1*, *2*, *3*, *4*). Lake at Mt. Cenis, 1900 m, 1963, R. Weibel (G). *Haute-Savoie:* Mt. Mirantin, Aut-du-Pré, at dried out pools, 1858, E. Perrier (BM, K, P, *2*, *4*). At Lac de Montriond, 1864, Delavay (K, *4*) and 1899, J. Briquet (G). At Lac de Gers, 1904, J. Briquet (G, *1*, *2*, *3*, *4*). On N. side of Mt. Jallouvre, at small lake, 1948, A. Zimmerman (G).

Switzerland

Unterwalden: Frutt, 1900 m, at pool, 1893, J. Hanhart (ZT). *Valais:* Lac de Fully, shores of the upper lake, 2200 m, 1880, H. Romieux (G); 1881, J. C. Ducommun (ZT); W. shore, 2129 m, 1913, H. Gams (IB). Probably near Brig, 1885, E. S. Marshall (BM). Alps at Vouvry, Tanay, 1898, P. Chenevard (G, *1*, *2*, *3*, *4*); at Lac de Tanay, 1899, J. Briquet (G). Plaine de Barterin, margins of pools, 1500 m, 1904, J. Briquet (G, *1*, *4*). Combe valley, below Seex, Crot-aux-Chiens, 1500 m, pool, 1920, J. Briquet (G, *1*, *2*, *3*, *4*). Bagnes valley, at lake below Boussine, 2000 m, 1918, H. Romieux (G). Mt. Zermatt, Findelen Glacier, Grünsee, 2500 m, sandy shore, 1923, L. V. Lester-Garland (K, *1*, *4*); shore of L. Grünsee, 2316 m, 1944, A. Becherer (G, *1*, *4*); Hotel Schwarzsee, 2582 m, sandy places, 1945, A. Becherer (G, *1*, *4*). *Graubünden:* Lenzerheide, 1832, herb. Moritzi (CHUR); at the lake, 1832, U. A. v. Salis (ZT); c. 1450 m, 1849 and without date, C. Brügger (CHUR, ZT), 1855, herb. Theobald (CHUR). Oberengadin, Samedan, 1725 m, 1844, U. A. v. Salis (ZT); Samedan, 1837, Moritzi (CHUR, *4*) and 1886, H. E. Fox (OXF, *2*, *4*); Albula, 1866, L. Favrat (ZT); Ponte, 1874, Anon. (ZT); At R. Inn between Ponte and Bever, 1700 m, 1881, C. Brügger (ZT); Cresta Celerina, 1910, H. Gams (IB); St. Moritz, 1915, A. Branger (ZT). Arosa, 1856, Killias (CHUR, *4*). Berninapass, 2170 m, 1905, Braun (G). Parpan, 1600 m, pool, 1918, L. Meisser (CHUR, *4*). Heinzenberg, Anon. (CHUR, *2*, *4*). San Bernardino, at stream in Rheinwald, 2065 m, 1838, U. A. v. Salis (ZT); Rheinwald, 1867 and without prec. loc., 1887, C. Brügger (ZT); at dried up pools, 1872, Favre (ZT).

Italy

Lombardia: Bormio, Passo delle Scale, at temporary lake, c. 1975 m, 1882, E. Cornaz (G, ZT) and c. 1915 m, 1887, E. Cornaz (K). *Trentino–Alto Adige:* Pusteria, Sesto, 1300–1500 m, Ausserdorffer (K); alps at Winbach, 2000–2300 m, Ausserdorffer (K, *1*, *4*). Above San Martino di Castrozza, 1867, J. Ball (E). [San Pellegrino, and Mt. Bondone, Gelmi (1898). Mt. Rovere, Gelmi (1900). Alps at Seis (Siusi), Murr (1897)].

Greenland

Julianehåb Distr.: Tunugdliarfik, "in stagnis subexsiccatis", Sagmesok, 1828, and without prec. loc. and date, J. Vahl (C, S, UPS, *1*, *2*, *3*, *4*); Qagssiarssuk (Brattahlið), 1925, A. E. & M. P. Porsild (C, GH) and 1926, H. Faum (C), towards Sermilik at small lake, 1937, J. Gröntved No. 924 (C); Tasiussaq, 1948, J. Gröntved (C); Musevikke-loc. between Qagssiarssuk and Tasiussaq, 1956, C. A. Jörgensen No. 148 (C); 2–3 km W. and 2.5 km S.W. of Qagssiarssuk, lake shores c. 100 m s.m., 1962, B. Fredskild Nos. 2162, 2287, moist ground at "road" from Qagssiarssuk to Tasiussaq c. 150 m, 1962, B. Fredskild No. 2137 (*2*, *4*) and Narssaq, moist ground, 1962, B. Fredskild No. 2185 (all in Nationalmuseet, Köbenhavn); Qagssiarssuk, 1937, N. Polunin Nos. 10997, 11024 and 11026 (OXF). *Holsteinsborg Distr.:* S. Strömfjord, at small lake at the river to N. arm of the firth, 1884, J. A. D. Jensen (C, UPS).

R. islandica* ssp. *dogadovae

U.S.S.R.

Saratovskaya obl.: Khvalinsk, at R. Volga, 1919, K. J. Gross No. 438 (LE, *1*) and 1927, K. Wysocz (LE); opposite Volsk, at R. Volga, 1916, M. G. Popov (LE, *1*). *Volgogradskaya obl.:* Krasnoarmeysk (Sarepta), herb. Kühlewein (UPS), at R. Volga, 1879, and without dates, A. Becker (BM, K, LE, *1*). *Astrakhanskaya obl.:* delta of R. Volga, S. Korzhinskiy (LE). *Kazakhstan:* Redutsk region, S. of R. Sarayczik, 1927, Z. Korovnik & T. Poyarkova No. 237 (LE, *1*). Near Uralsk, at R. Ural, 1925, T. F. Poyarkov No. 280 (LE, *1*). Kachiry, at R. Irtysh, 1942, N. V. Pavlov No. 33 (LE, *1*). Near Pavlodar, moist sandy shore of R. Irtysh, 1955, A. Dogadova & N. Tzvelev No. 852 (Gerb. Fl. SSSR No. 4115, BM, K, LE, S, *1*). *Tyumen obl.:* near Tobolsk, at R. Irtysh, 1906, Mameev No. 162 (K, *1*). *Altayskiy Kray:* Rubtsovsk region, Veseliy Yar, at R. Aley, 1924, V. I. Vereshczagin (LE, *1*). *Tomskaya obl.:* Narym, at R. Ob, 1898, H. Stenberg (H, *1*). *Krasnoyarskiy Kray:* Nikandrovskiy ostrov in R. Yenisey 70° 10′ N, 1875, A. N. Lundström (H, S, UPS, *1*), 1876, M. Brenner (S, UPS); at mouth of R. Kureyka into R. Yenisey 66°31′ N, 1914, N. I. Kusnezow & V. V. Reverdatto No. 4101 (C, BM, *1*).

Appendix 3. Collections of *Rorippa palustris*

Only for some regions of special interest a greater number of herbarium specimens are listed. These regions are N. Norway (NTrd-Fnm), N. Finland (Le, Li, Lpt, Ks), Russian Fennoscandia (northern parts), Scotland, Ireland, the Alp region (Switzerland and adjacent parts of France, Italy and Austria), central and northern Russia, western Siberia, and Greenland. From other regions chiefly only specimens used in diagrams are included. All specimens listed from U.S.A. and Canada have been used in Fig. 9. For these the subspecies are indicated as follows: *f.* = ssp. *fernaldiana*, *h.* = ssp. *hispida*, *p.* = ssp. *palustris; f.-h.* etc. indicates intermediate specimens. All material listed from other regions belongs to ssp. *palustris*. For further explanations see p. 167.

Denmark (specimens used in diagrams)

J 876 (*2*), 885 (*2*, *9*), 1441 (*9*), 1449 (*9*), 1547 (*9*), 1554 (*9*), 1557 (*9*), 1558 (*9*), 1563 (*9*).

Sweden (specimens used in diagrams)

Sk: Hässleholm, 1882, K. F. Dusén (UPS, *9*). *Vg:* Vänersborg, 1938, J. E. Palmér (UPS, *9*). *Nrk:* Knista, Brotorp, 1920, T. Hellsing (UPS, *9*). *Srm:* Nämdö, Långeskär, 1918, C. G. Alm (UPS, *9*). *Ång:* Härnösand, 1906, T. Tengvall (UPS, *9*). *Hrj:* Linsäll, Slöte, 1916, G. Cedergren (UPS, *9*). *Jtl:* Fors, by R. Indalsälven, 1946, S. O. Björkman No. 931 (UPS, *9*). Hammerdal, Fyris, L. Solbergsvattnet, 1948, T. Roos (UPS, *9*). *Nb:* Älvsby, Älvsbyn, 1917, C. G. Alm (UPS, *9*). *TL:* Jukkasjärvi, Björkliden railway station, 1924, C. G. Alm (UPS, *9*). J 137 (*4*, *9*), 140 (*4*), 142 (*1*, *2*, *3*, *4*, *9*), 145 (*9*), 146 (*9*), 147 (*9*), 169 (*4*), 170 (*4*, *9*), 172 (*4*, *9*), 174 (*9*), 175 (*1*, *2*, *3*, *4*, *9*), 177 (*4*, *9*), 176 (*4*), 181 (*4*), 182 (*4*, *9*), 183 (*9*), 184 (*4*, *9*), 187 (*1*), 190 (*4*, *9*), 192 (*4*, *9*), 193 (*4*), 254 (*2*, *4*, *9*), 343 (*4*), 350 (*4*, *9*), 364 (*4*, *9*), 369 (*1*, *2*, *3*), 377 (*1*, *2*, *3*, *4*, *9*), 380 (*4*, *9*), 391 (*4*, *9*), 516 (*4*, *9*), 524 (*9*), 529 (*4*, *9*), 548 (*4*), 621 (*2*), 855 (*1*, *2*, *3*, *4*, *9*), 864 (*2*), 899 (*2*, *9*), 922 (*2*, *9*), 938 (*2*, *9*), 946 (*2*, *9*), 949 (*2*), 1071 (*9*), 1077 (*9*), 1078 (*9*), 1079 (*9*), 1080 (*1*, *2*, *3*, *9*), 1093 (*9*), 1102 (*1*, *2*, *3*, *9*), 1105 (*9*), 1117 (*1*, *9*), 1139 (*2*), 1267 (*9*), 1387 (*9*), 1389 (*9*), 1394 (*9*), 1456 (*1*, *3*, *9*), 1504 (*2*), 1507 (*2*), 1522 (*2*), 1572 (*2*, *4*, *9*).

NORWAY

Nord-Tröndelag: Namsos 1890, Anon. (TRH); 1896, O. A. HOFFSTAD (O); 1953, H. H. VOGNILD (TRH). Harran, Fiskum, roadside, 150 m, 1913, J. GJERSTAD (TRH); Gastland, 160 m, 1953, J. GJERSTAD (TRH); Fjerdingen, weed in a field, and Moa, 100 m, both 1954, J. GJERSTAD (TRH, *9*). Frosta, Liavandet, 1914, I. JÖRSTAD (O). Steinkjer, railway station, 1950, H. RUI (O). Stjördal, Stjördalshalsen, 1917, A. NOTÖ (TRH, TROM, *9*); Berri, 1954, J. GJERSTAD (TRH). Foldereid, Arebrot, shore, 1935, K. STROMPDAL (O). Grong, garden, 1945, P. BENUM (TROM). Hegra, Bjugan, 1950, J. GJERSTAD (TRH, *9*); Damtjörna, 1951, J. GJERSTAD (TRH). Höylandet, Tyldum, and Grangestad, at farm, both 1952, J. GJERSTAD (TRH). Röyrvik, Vellervatn, 1955; E. of Krosnes, 490 m, 1955; W. of the church, 430 m, 1956, all J. GJERSTAD (TRH). Meråker, near Kopperåsen railway station, 325 m s.m., 1958, T. OUREN (TRH). *Nordland*: Bindal, Årsandöy, roadside, K. STROMPDAL (O). Vefsn, Halsöy, Kråkdalene, roadside, 1927, P. BENUM (TROM); Alsgård, 1947, G. & K. STROMPDAL (TRH). Mosjöen, Skjervengane, garden, 1944, P. BENUM (TROM). Lödingen, Ö. Kåringvatn, new dam, 1948, J. REIESSEN (TRH). Velfjord, Hilsted, field, 1950, K. STROMPDAL (TRH). Melöy, Glomfjord, Hangvik, 1944, H. SCHULZ (TROM). Hadsel, garden weed, 1944, P. BENUM (TROM). J 525 (*4*). *Troms:* Målselv, Lerbakmo, 1869, NORMAN (O), Moen, 1884, NYHUUS (O); Andsvatn, roadside, 1946, P. BENUM (TROM); Fleskmo, German hutments, 1946, P. BENUM (TROM); Rundhaugen, Kirkesnes, ditch, 1948, P. BENUM (TROM, *9*); J 484 (*1, 3, 4, 9*), J 486. Bardu, between Sætermoen, and Ala, 1879, J. M. NORMAN (O); Högda, 1885, J. R. LANDMARK (TROM), *9*). Nordreisa, Punta, 1932, Y. MEILAND (O). Tromsö, in the town, 1934, P. BENUM (O, TROM). Salangen, Salangsverket, 1949, P. BENUM (TROM). *Finnmark:* Alta, Bossekop, 1821, J. W. ZETTERSTEDT (LD); near Vina, road, 1900, 1903, O. DAHL (O). Tana, Fingervatnet and at Tana R., 1855, C. SOMMERFELT (O, UPS); at Tana R., 1857, TH. M. FRIES (O, UPS); between Banak and Fjelmanes, 1935, J. A. NANNFELDT (UPS); J 499 (*1, 2, 3, 4, 9*), J 504. Karasjok, Anarjokka, at the uppermost settlement, 1861, J. M. NORMAN (BG); Oudsessanjarga, 1864, J. M. NORMAN (BG, O, TRH, UPS, *9*), 1882, G. BALKE (TROM). Polmak, at Polmak R., 1900, 1901, O. DAHL (O); moist sand, 1939, R. NORDHAGEN (BG). Sör-Varanger, Nedre Klistervatnet and Pasvik R., J. M. NORMAN (O); Svanvik and Pasvik, Melkefossen, 1917, O. DAHL (O); Övre Pasvik, 1924, Salmijärvi, 1927, Neiden, 1927, all WESSEL (TROM, *9*); Salmijärvi, 1937, T. SOOT-RYEN (TROM); Skogfoss, brook, 1949, N. HAUGE (O); between Solls and Nygård, "German" road, 1950, P. BENUM (TROM). Kistrand, Banak, 1949, P. BENUM (TROM, *9*).

Specimens from other prov. used in diagrams: *Östf:* Onsöy, 1901, Herb. RYAN (TRH, *9*). Moss, mill, 1958, T. OUREN (TRH, *9*). *Vestf:* Sandefjord, 1910, B. STRÖM (TROM, *9*). Tjölling, Eftang, 1927, O. A. HÖEG (TRH, *9*). *VAgd:* Lista, Tjörve, 1947, P. STÖRMER (O, *9*). *Rog:* Karmöy, Avaldsnes, 1933, V. ROSSELAND (O, *9*). *Hrd:* Voss, Rognsfossen, 1960, J. LID (O, *9*). *STrd:* Orkedalsören, 1900, F. LANGE (TRH, *9*). Buvik, Pienes mill, 1927, O. A. HÖEG (TRH, *9*). Flå, 1948, Bot. For. Eks. (TRH, *9*). Singsås, Almås, 1956, T. OUREN (TRH, *9*). Singsås, Råen, 1957, T. OUREN (TRH, *9*). Opdal, Drinstua railway station, 1957, H. RUI (O, *9*). Strinda, Sluppen, 1959, E. FONDAL (TRH, *9*). J 939 (*2*), 940 (*2, 9*), 941 (*2*), 950 (*1, 2, 3, 9*).

FINLAND

Lapponia enontekensis: Enontekiö, Kelottijärvi, Saarenpää, 1939, A. PAALANEN (H) and J. I. LIRO & H. ROIVAINEN (H); Könkämäeno, Kelottijärvi, Uusitalo, 1939, H. ROIVAINEN (H); Karesuanto, Muoniojoki, 1947, E. J. VALOVIRTA; Rapinsalmi, 1958, R. L. HÄMET (H). J 1118 (*9*), 1120. *Lapponia inarensis:* Inari, Kyrö, 1802, herb. WAHLENBERG (UPS); Lentolahti, 1870, F. SILÉN (H); Martti at L. Inari, 1880, A. ARRHENIUS & A. O. KIHLMAN (H); 1909, A. RENVALL (H, *9*); Sevettijärvi, Varpuniemi, 1951, L. OLLILA (H). Utsjoki, Karigasniemi, Outakoski, 1954, R. NIKOSKELAINEN (TUR). J 509 (*2, 4, 9*), 510 (*1, 2, 3*), 511 (*4, 9*). *Lapponia petsa-*

moënsis: Petsamo, Alaluostari, 1927, A. Cajander (H); Kuvernöörinkoski, 1929, T. Kontuniemi (H, *9*); Salmijärvi, 1932, A. V. Auer (TUR). *Kuusamo:* Kantoniemi, 1877, E. Wainio (H). Oulankajoki, Merenoja, 1908, A. L. Backman (H); near Kiutakönkä, 1930, K. Linkola (H, *8*); Liikanen, 1957, Y. Vasari (H, *9*). Kuolajärvi, Jyrhämäjärvi, 1917, V. Pesola (H); Kutsajokialue, 1925, K. Linkola (H). Taivalkoski, Jurmu, 1948, O. Lehtonen (H). J 465 (*2, 9*).

Specimens from other prov. used in diagrams: *Lk:* Muonio church village, 1917, J. Montell (H, *9*). Sodankylä, Suranto, 1927, A. Cajander (H, *9*). Kittilä, Mustavaara, 1956, R. Ruuhijärvi (H, *9*). J 402 (*2, 4, 9*), 403 (*4, 9*), 405 (*4, 9*), 408 (*2*), 410 (*1, 2, 3*), 440 (*4, 9*), 442 (*1, 2, 3, 4, 9*), 466 (*2, 4, 9*), 468 (*2, 4, 9*), 469 (*9*), 471 (*4, 9*), 472 (*4, 9*), 473 (*4, 9*), 475 (*9*), 514 (*2, 4, 9*), 515 (*2, 4, 9*), 518 (*2, 4, 9*), 959 (*9*), 1119 (*9*), 1133 (*9*), 1299 (*2, 9*), 1300 (*9*), 1301 (*9*), 1302 (*9*), 1303 (*9*), 1304 (*9*), 1305 (*9*), 1440 (*9*), 1458 (*9*), 1459 (*9*), 1481 (*1, 3, 9*).

Russian Fennoscandia

Lapponia murmanica: Jokenga "basa", 1927, E. Hultén (S). *Lapponia tulomensis:* Near mouth of R. Nuotjok, Hyötösaari, 1891, J. Lindén (H). Murmansk, 1927, E. Hultén (S). *Lapponia Imandrae:* Pore Guba, 1861, G. Selin (H). L. Nuortijaur, 1883, R. Enwald & H. Hollmén (H). Mouth of R. Seidjok, and at L. Lujawr, both 1887, A. O. Kihlman (H, *2*). Hirvasjärvi, 1901, W. M. Axelsson & V. Borg (H, *9*). Monche Tundra region, 1939, A. N. Yegorov No. 152 (LE). At L. Imandra, 1957, T. Yegorova (LE, *2*). *Lapponia Varsugae:* Kamensk at R. Ponoy, 1887, J. A. Palmén (H, S). Tshupoma, at the river, 1889, A. O. Kihlman (H, *9*). *Lapponia ponojensis:* Ponoy, shore opposite the village, 1899, J. Montell (H, TURA). *Karelia keretina:* Kontajärvi, 1861, N. J. Fellman (H).

Great Britain

England (specimens used in diagrams). *E. Cornwall:* Lostwithiel, by Forvey R., 1901, O. O. Hume No. 3792 (SLBI, *2, 4, 9*). *N. Somerset:* Shopwick, 1885, J. W. White (OXF, *9*). *Surrey:* Wandsworth Common, 1842, herb. Wilson Saunders (OXF, *4, 9*). *Oxfordshire:* Clattercut, Northants, G. C. Druce (OXF, *4, 9*). *N. Lancashire:* Oldcliffe, 1838, Anon. (OXF, *2, 4, 9*). *Monmouthshire:* Usk, by R. Usk, 1941, S. G. Charles (NMW 41·237·11, *9*).

Wales (specimens used in diagrams). *Glamorgan:* Cardiff, Splott, 1929, A. E. Wade (NMW 30·33·24, *2, 4, 9*). *Breconshire:* Llangorse Lake, 1925, A. E. Wade (NMW 25·530·62, *2, 4, 9*). *Radnorshire:* Erwood, by R. Wye, 1929, A. E. Wade (NMW 30·35·25, *2, 4, 9*). *Carmarthenshire:* Llandillo, 1921, D. Hamer (NMW 24·470·1, *2, 4, 9*). *Montgomeryshire:* by Vyrnwy R., 1940, J. A. Webb (NMW 40·286·22, *9*).

Scotland. *Dumfriesshire:* Lochmaben, 1877, comm. Reid (E). *Kirkcudbrightshire:* 1839, J. Cruickshank (E). *Ayrshire:* Dundonald, herb. Kropp (E). *Lanarkshire:* Banks of Clyde, near Glasgow, 1837, D. Slim (E). N of Glasgow, herb. Brodie (E). *Peebleshire:* by R. Tweed, 1888, G. C. Druce (OXF, *4, 9*). *Roxburgshire:* Melrose, by R. Tweed, 1894, C. Bailey (OXF, *2*). *East Lothian:* Dirleton, 1835, herb. Balfour (E, *2*). 1835, comm. Macnab (E, K). *Midlothian:* Near Portobello, 1834, herb. Balfour (E) and 1835, G. Macnab (BM). Duddingston Loch, 1821, herb. Greville (E), 1869, W. Evans (E, *2*) and 1893, herb. Terras (E). J 1294 (*2, 4, 9*). *West Lothian:* Linlithgow Loch, 1838, herb. Balfour (E, UPS) and herb. Campbell (E); 1904 herb. Adamson (BM, *2*). *Fifeshire* (with Kinross): Loch Leven, 1832, Wright (E); 1905, G. T. West (E); 1912, G. C. Druce (OXF); Arnott (K). *West Perthshire* (with Clackmannan): W. of Dollar, 1905, W. Evans (E). *Mid Perthshire:* Perth, 1891, E. F. Linton (BM); harbour, 1897, R. H. Meldrum (E). *East Perthshire:* Blairgowrie, Stormont Loch, 1906, E. S. Marshall (CGE, BM, E, *2, 4*) and 1951, 1953, D. M. Henderson (E). Near Meikleour, 1887, R. H. Meldrum (E). *Angus:* 1837, Reid (E). Montrose, 1834, herb. Balfour (E). Forfar

Loch, 1834, herb. Balfour (E). Near Forfar, G. Don (E). *Dumbartonshire:* Hardgate Dam near Clydebank, 1910, W. E. Evans (E). *Shetland Islands:* Olna Firth, 1924, G. C. Druce (OXF).

Ireland

S. Kerry: Killarney, Ross Bay, 1887, R. W. Scully (DBN). *N. Kerry:* Farranfore, Ardcrone, swamps, 1903, R. W. Scully (DBN). *W. Cork:* Clonakilty Junction, 1930, R. A. Phillips (DBN). *E. Cork:* Fermoy, by R. Blackwater, 1851, herb. Chandlee (DBN); 1885, R. Vowell (DBN). *Waterford:* Lough Cullen, 1871, R. M. Barrington (DBN). *Clare:* Ballyvaughan, 1885, R. P. Murray (BM). *N. Tipperary:* Templemore, 1898, R. L. Praeger (DBN). Killaloe, roadside, 1899, R. L. Praeger (DBN, *2*). Near Thurles, river bank, 1961, M. Mc Collum-Webster (K). *Kilkenny:* Lough Cullen, boggy lake margin, 1898, R. L. Praeger (DBN). *Wexford:* New Ross, 1892, L. Glascott (DBN). Enniscorthy, wet riverside, 1898, R. L. Praeger (DBN); R. Slaney, herb. Hart (DBN). *N.E. Galway:* Headford, bog Abbey of Ross, 1832, herb. Shuttleworth (BM, *2*). Near town of Galway, roadside, 1884, H. C. Levringe (DBN, K) and Killower Lake, and Tuam, by R. Clare, 1899, both R. L. Praeger (DBN). *Offaly:* Banagher, by R. Shannon, 1898, R. L. Praeger (DBN). Portarlington, river bank, 1906, R. L. Praeger (DBN). *Wicklow:* Mizen Head, 1925, A.W.S. (DBN). *Dublin:* Lusk, ditch bank, 1893 and Balrothery, shore, 1893, N. Clogan (DBN, *2*). Blackrock, drains by railway, 1902, N. Clogan (DBN). Naul, marshy ground, 1953, M. P. Scannell (DBN, *2*). Garristown, herb. Hart (DBN). *Meath:* Oldcastle, river edge, 1896, R. L. Praeger (DBN, *2*). *Westmeath:* Lough Ennil, 1891, H. C. Levringe (DBN), and 1957, M. Scannell (DBN). S. of Lough Derravaragh, 1950, D. A. Webb (K, S). *Roscommon:* Lough Ree, 1885, R. M. Barrington (DBN). Mt. Talbot, river banks, 1891, H. C. Levringe (DBN). Near town of Roscommon, roadside, 1903, T. A. P. Mapother (DBN). *Leitrim:* Fenagh, bog, 1868, herb. Beresford (DBN). Carrick on Shannon, marshy ground, 1899, R. L. Praeger (DBN, *2*). *Cavan:* Lough Oughter, 1905, R. L. Praeger (DBN). *Fermanagh:* Lough Erne, Devenish Isl., 1882, herb. More (DBN). *Tyrone:* herb. Steele (DBN). *Armagh:* J 1175 (*2, 4, 9*), J 1177. *Down:* Ballievey, 1854, E. Malone (DBN). Newtownards, 1866, S. A. Stewart (BM); Kiltonga, marshy ground, 1944, R. M. Meikle (K). *Antrim:* Belfast, 1873, S. A. Stewart (BM); Lagan Banks, 1882, R. T. Vowell (DBN, *2*). Lough Neagh near Shanes Castle, 1874, R. Barrington (DBN). *Londonderry:* Kilrea, by R. Bann, 1894, R. L. Praeger (DBN).

Netherlands: J 1145 (*2*)

Germany

Württemberg: Radolfzell, Moos, at L. Untersee (Bodensee), 1906, E. Baumann (ZT, *1, 4, 9*); Mettnau, at L. Untersee, 1905, E. Baumann (ZT). Iznang, at L. Untersee, 1905, E. Baumann (ZT). J 1134, 1298 (*2, 9*), 1461, 1468 (*1, 3*), 1586, 1591.

France

Haute-Garonne: Portet, by R. Garonne, 1847, Anon. (TL, *1*) and 1906, Sudre (TL). Toulouse, by R. Garonne, 1855, M. Loret (P), 1870, H. Chalande (TL); Anon. (TL, *1*). St. Béat, Estagneau, 1856, J. E. Zetterstedt (UPS). *Ain:* Bourg, 1880, J.-P. Fray (Exs. distr. Société dauphinoise, 1881, No. 2750). *Vosges:* Rambersville, by R. Mortagne, 1893, C. Claire (Fl. selecta exs. distr. Ch. Magnier, No. 3197). *Indre-et-Loire:* Near Tours, by R. Loire, 1856, J. Delaunay (Fl. Galliae et Germaniae exs. distr. C. Billot, No. 2012). — J 957 (*2, 9*), 1073, 1136 (*2, 9*), 1297 (*2, 9*).

Switzerland

Genève: 1873, E. Ayasse (UPS). *Vaud:* Villeneuve, 375 m, 1869, L. Favrat (ZT, *1*, *4*, *9*). Roche, marshes, 350 m, 1815, E. Thomas (ZT, *4*, *9*). "Udis prope Villeneuve", Anon. (IB). Orbe, 445 m, 1868, L. Favrat (ZT). Lausanne, Cour, 420 m, 1880, L. Favrat (ZT). *Neuchâtel:* Ouchy, herb. Leresche (BM). Town of Neuchâtel, Maisonrouge, 1847, G. Jeanjaquet (ZT, *4*, *9*); 1879, G. Jeanjaquet (ZT, *4*, *9*). Village Schüle, 1849, G. Jeanjaquet (ZT, *4*). *Bern:* Kaeferfeld, 1924, R. la Nicca (CHUR, *2*, *4*, *9*). Münchenbuchsee, 1918, R. la Nicca (CHUR, *2*, *4*, *9*). *Baselland:* Basel, F. Bernoulli (ZT); Neudorf, 240 m, M. Rikli (ZT). *Aargau:* Entfelden S. of Aarau, 424 m, 1848, I. Müller-Arg. (ZT, *4*, *9*). Zofingen, 1877, H. Siegfried (ZT). *Zürich:* Near city of Zürich, Enge, 1815, Schultess (ZT), 1885, E Ruhoff (ZT) and without date, A. Kölliker (ZT); 1839, herb. Vogel (ZT); 1837, herb. Scm. Unterstr. (ZT); 1877, Anon. (ZT); Bellevoir Enge, 413 m, 1899, A. Keller (ZT); Brauerei Uto, 430 m, 1899, M. Rikli (ZT, *1*); Sihlfeld, 1890, R. Rau (ZT). Kappel, 1880, Hegelschneider (ZT, *1*). Andelfingen, L. Grossee, 400 m, 1882, E. Landolt (ZT). Buchs, 1903 and 1904, M. Rikli (ZT, *4*, *9*). L. Pfäffiker See, M. Rikli (ZT, *4*, *9*). Wallisellen, 1917, E. Baumann (ZT). *Schaffhausen:* Neuhaus, 436 m, 1860, G. Schalch (ZT, *1*, *4*). Anon. (CHUR, *9*). *Thurgau:* Frauenfeld, 1891, Anon. (ZT). Gottlieben at L. Untersee (Bodensee), 1906 and 1907, E. Baumann (ZT). *Schwyz:* Einsiedeln, 900 m, 1861 and without date, C. Brügger (ZT); 900 m, 1904 and without date, M. Rikli (ZT, *4*, *9*); Roblosen, 880 m, 1902, M. Rikli (ZT) and 1909, E. Hess (ZT, *1*, *4*, *9*). *Glarus:* Gäsi, 425 m, O. Heer (ZT). *St. Gallen:* Wallenstadter See, 1831, U. A. v. Salis (ZT, *9*). *Valais:* Marais de Vouvry, 380 m, 1875, herb. L. Favrat (ZT). Lac de Morgins, 1300 m, 1905, J. Briquet (G, *4*, *9*). Branson, herb. Cavin (G). Bouveret, herb. Cavin (G, *2*). *Ticino:* Locarno, at L. Maggiore, 1845, A. Franzoni (ZT); delta of R. Maggia, 1918 and 1919, M. Jäggli (ZT, *1*, *4*, *9*). Lugano, 1919, A. Voigt (ZT). *Graubünden:* Rheinwald, 1400–1450 m, Felix (ZT). La Rofna, 1857, herb. Lorez (CHUR, *2*, *4*, *9*). Ardez, 1870, Killias (CHUR, *2*, *4*, *9*). Laax, 1023 m, 1882, C. Brügger (ZT). Ilanz, 1911, K. Hager (ZT). Roveredo, 1911, herb. Hatz (CHUR, *4*, *9*). Bonaduz, 670 m, 1914, herb. Hatz (CHUR). Oberengadin, Celerina, 1916 and 1917, A. Branger (CHUR, ZT, *2*); Poschiavo, La Rosa, Anon. (CHUR, *4*, *9*); Cavaglia, 1700 m, railway station, 1921, L. Meisser (CHUR). Laret, at factory, 1926, P. Flütsch (CHUR). Landquart, paper factory, 1931, P. Flütsch (CHUR, *2*). Igis, 1931, herb. Hatz (CHUR, *4*, *9*). Zerniz, pool by R. Inn, 1954, P. Müller-Schneider (CHUR, *1*, *4*, *9*). J 1566 (*2*).

Italy

Piemonte: Cúneo, 1880, herb. Pozzi (ZT). *Lombardia:* Between Morbegno and Cólico, 1868, C. Brügger (ZT). Near Cólico, 1912, P. Chenevard (G, *4*). Sondrio, near railway station, 1913, P. Chenevard (G, *4*, *9*). Passo d'Aprica, 1250 m, 1910, P. Chenevard (G, *1*, *9*). *Trentino–Alto Adige:* Bolzano (Bozen), 1854, Hausman (IB, W, *4*, *9*) and without date, herb. Pittoni a Dannenfeldt (W). Lutago (Luttach), 1100 m, 1880, G. Tufferl (W, *4*, *9*). Landro, 1895, Saint-Lager (G, *2*, *4*, *9*). *Emilia:* Prov. of Ferrara, by R. Po near Pontelagoscuro, 1912, A. Ferioli (Fl. Italia exs. ser. II, No. 1675, *4*, *9*).

Austria

Tirol: Innsbruck, Schmuchl (IB); in corn, 570 m, 1878, S. J. Menyhárth (G, *1*, *4*, *9*). St. Anton, gravelly slope at the tunnel, 1320 m, 1906, E. Preissmann (W). Zillertal, Mayrhofen, 1911, E. Saint-Lager (G, *4*, *9*). Göttingstein, 1920, R. Berger (IB, *4*, *9*). *Ost Tirol:* Near Lienz, by R. Drau, 1872, Garder (K, *2*, *4*, *9*). *Kärnten:* Villach, 530 m, 1881, E. Preissmann (W); 1886, E. Witting (W, *4*, *9*); 1934, K. Dick (IB). *Steiermark:* leg. Gebhard (W, *4*, *9*). Ettendorf near Stainz, 325 m, 1906, P. v. Troyer (Fl. stiriaca exs., distr. v. Hayek, No. 849).

Aschbach near Wegscheid, 900 m, 1910, A. Klammerth (Fl. stir. exs. No. 1286, *4*, *9*). Waltendorf near Graz, 350 m, 1887, E. Preissmann (W). Krollendorf railway station, 360 m, 1891, E. Preissmann (W, *4*, *9*). Stiftingthal near Graz, 410 m, 1892, E. Preissmann (W). Söchau, at pools, 1908, H. Sabransky (W, *4*, *9*). Pragerhof, 250 m, 1877, E. Preissmann (W). Radkersburg, by R. Mur, 210 m, E. Preissmann (W). Admont, 1875, G. Strohl (W). Graz, 1867, J. C. Pittoni a Dannenfeldt (W). Voitsberg, J. C. Pittoni a Dannenfeldt (W). J 1455 (*1*, *2*, *3*). *Oberösterreich:* Haslach, Klettgau, 1911, H. Gams (IB, *1*, *4*, *9*). *Burgenland:* Neuschützen, meadows, 1932, E. Korb (UPS).

Yugoslavia

Slovenija: Ljubljana (Laibach), 300 m, moist, sandy places (Fl. exs. carniolica No. 465, *2*, *4*, *9*).

Czechoslovakia

Moravia: Brno region, Lednice (Eisgrub), 1910, W. Zimmerman (Fl. Bohemiae et Moraviae exs. distr. F. Petrak, Lfg V, No. 452, *2*, *4*, *9*). *Bohemia:* Praha region, Beroun distr., Nižbor, 220 m, 1960, J. Sajàk (Pl. Čechosl. Exs. No. 181, *4*, *8*). J 1470. – J 954 (*9*).

Poland: J 1467 (*2*).

U.S.S.R. (except Russian Fennoscandia)

Esthonia: Reval, herb. Russow (LE). Hiumaa (Dagö), Emmast, 1871, C. Winkler (LE); Dagerort, on sea-wrack, 1926, O. Eklund (H); Küla and Mänspea, sandy beaches, 1939, J. Gröntved Nos. 1680, 1681 (C). Peipus region, Pietrisaar, 1921, E. Lundström No. 677 (S). Harjumaa, Kuusalu, river mouth, 1922, G. Vilberg (TUR). Vormsi (Wormsö), Söderby, 1924, J. Gröntved (S). Yygevamaa, Tiarivere, 1950, E. Parmasto (LE). *Pskovskaya obl.:* Near L. Dubets, Oparino, 1915, N. I. Kuznetsov No. 331 (S). Ostrov region, Berezhansk, 1921, and Kalanov, 1929, F. L. Zhirnov (LE). Serebryansk, by R. Plyussa, 1923, G. Zinserling (LE). *Leningradskaya obl.:* By R. Luga near Kemk, 1911, D. Litvinov (LE). Semrino, 1919, E. Czerniakovska (LE). Near Vyritsa, 1939, A. G. Borisova No. 241 (LE). J 1280 (*2*). *Vologdayskaya obl.:* Vytegra distr., Samik R. near Maksimov, 1926, J. Suchowa (LE, S). *Arkhangelskaya obl.:* Krasnoborsk, 1891, A. O. Kihlman (H). Glauchavski Isl. in R. Dvina, railway station, 1911, S. J. Enander (S); Siya, near R. Dvina, 1912, S. J. Enander (S). Mouth of R. Peczora, Zapetczerski Isl. near Kuya, 1912, S. J. Enander (S). Arkhangelsk, near wireless station, 1919, W. S. Goodhew (BM, *2*). Kotlas region, by R. Vychegda, 1927, A. Selivanova (LE). Malozemelskaya tundra, region around the rivers Neruta and Seduika, 1930, A. Dedov & K. Shaparenko No. 644 (LE). Kanin peninsula, central part, by R. B. Sobacz, 1945, V. Matveev (LE). Bolshezemelskaya tundra, basin of R. Chalmer-Yu, 1958, A. I. Tolmaczev & O. V. Rebristaya (LE). *Komi ASSR:* Koygorodsk, by R. Sysola, 1908, V. Andreev (LE). Basin of R. Kozhva, 1935, A. I. Leskov & I. F. Maskil No. 104 (LE). Intinsk region, Sivaya Maska, 66°40′ N, 62°30′ E, 1960, V. ? (LE). Vozkuta, near coal-mine, 1958, E. Dorogostaiskaya (LE, UPS). Khodaty, Polar Ural station B, 1962, S. Sandomirskaya (LE, UPS). *Kirovskaya obl.:* Kotelnikh (Orlov) region, 1917, A. Fokin No. 385 (LE). Kumena region, 1921, A. Zubarev No. 96 (LE). Near Kirov, 1921, E. Elin (S). *Orenburgskaya obl.:* Troitskoye distr., 1916, I. M. Krasheninnikov (LE). *Tyumen obl.:* Konda region, Makrovskiya, 1880, E. Vainio (TUR). *Novosibirskaya obl.:* Ubinskoye, railway station, 1913, S. J. Enander (S). *Tomskaya obl.:* Ob region, near Kalganakyi, 1898, H. Stenberg (H); Katelkyi, 1898, H. Stenberg (H). Near Kolyvan, 1916, P. E. Svinhufvud (H). *Krasnoyarskiy Kray:* Yenisey Valley between R. Pit and R. Middle Tunguska, 1866, J. Markjelov (BM). Nikandrovskiy Isl. in R. Yenisey, 1876, M. Brenner (H). 15 km above Dudinka, by R. Yenisey, 1876, H.

W. Arnell (UPS). Yeniseysk, 1876, Marks (S); 1914, S. J. Enander (S). L. Brekhovskiy Isl., 1876, H. W. Arnell (S). Minusinsk distr., 1885, Ehnberg & Hammarström (H, TURA); near Kushabar, 1914, H. Printz (H). By R. Yenisey at Jartovske and at Verkhne-Imbatskoye, 1914, S. J. Enander (S). Turukhansk distr., by R. Yenisey near Sumarokova, 1914, N. I. Kusnezow & V. V. Reverdatto No. 4227 (BM). Dudinka, ditch, Igarka, field, and Norilsk, garden, all 1959, E. Dorogostaiskaya (LE, UPS). – J 943 (*2*), 1075, 1225, 1539 (*1*).

Greenland

Julianehåb Distr.: Ivigtut, 1899, Lindhard (C); 1934, J. Lagerkranz (S); 1937, J. Grøntved No. 923 (C); 1946, T. W. Böcher No. 358 (C); 1954, A. Hemmingsen (C); 1957, S. Laegaard No. 576 (C); 1961, A. Pedersen (C). Arsuk, 1952, N. Kjölsen (C). Grönnedal, 1961, A. Pedersen (C).

United States

Maine: Kennebunkport, 1888, G. G. Kennedy (GH, *h.*). Piscataquis Co., Dover, 1895, M. L. Fernald No. 380 (GH, *h.*). Aroostook Co., Ft. Fairfield, 1893, M. L. Fernald (GH, MIN, type, cf. Ch. 8, *f.*); Masardis, 1897, M. L. Fernald (NEBC, *f.*).

Canada

New Brunswick: Charlotte Co., Grand Manan, 1934, C. H. Knowlton & C. A. Weatherby No. 6651 (DAO, GH, *h.*). York Co., W. of Fredericton, 1953, I. J. Bassett & G. A. Mulligan No. 2856 (DAO, *f.-h.*). Sunbury Co., S.E. of Fredericton, 1953, I. J. Bassett & G. A. Mulligan No. 2870 (DAO, *f.-h.*). *Prince Edward Islands:* Prince Co., Wellington, 1952, D. Erskine No. 1406 (DAO, *f.*). *Nova Scotia:* Cape Breton Co., Sydney Mines, 1920, C. H. Bissell & D. H. Linder No. 21327 (GH, *f.*); Cranberry Point, 1951, E. C. Smith *et al.* No. 5412 (DAO, *p.*). Cumberland Co., Soldier Brook, 1954, W. B. Schofield No. 5206 (DAO, *p.*). Victoria Co., Plaster Mines, 1956, E. C. Smith *et al.* No. 15009 (DAO, *f.* $2n = c.$ 32, Mulligan 1964). *Newfoundland:* Valley of Exploits River, Bishop Falls and Grand Falls, both 1911, M. L. Fernald & K. M. Wiegand No. 5485 and 5487 (GH, *h.*). Little Bonne Bay Pond, 1937, J. Risbeth No. 124 (BM, *f.-h.*). Arder Pond, 1938, C. A. Lister No. 62 (BM, *h.*). Labrador, Goose Bay, Goose River, 1950, J. M. Gillett & W. I. Findlay No. 5755 (DAO, *h.*); North West River, 1950, J. M. Gillett & W. I. Findley No. 5526 (DAO, *p.*). Humber Distr. Grand Lake, Hinds Brook Point, 1951, E. Rouleau No. 2284 (DAO, *f.-h.*). *Quebec:* Saguenay Co., Roberval, 1892, G. G. Kennedy (GH, *h.*); Lagorgendière, Romaine, 1915, H. St. John (GH, *f.*). L. St. Jean Co., 1904, W. Wright (GH, *h.*); Val-Jalbert, 1955, F. Rolland-Germain No. 7012 (DAO, *h.* $2n = 32$, Mulligan 1964). St. Maurice Co., Pointe du Lac, 1923, E. B. Chamberlain & C. H. Knowlton (GH, *h.*). Deux-Montagnes Co., La Trappe, 1926, P. Louis-Marie No. 121 (GH, *h.*). Joliette Co., Joliette, 1927, E. Roy (DAO, *p.*). Nicolet, 1927, Sœur St. Thomas d'Aquin (DAO, *f.-h.*). Longueuil, Ile Plate, 1928, F. Marie-Victorin No. 28286 (DAO, *f.*), and 1929, F. Rolland-Germain No. 29112 (DAO, *f.*). Chambly Co., Saint-Hubert, 1930, FF. Marie-Victorin & Romain-Rolland No. 33975 (DAO, *h.* GH, *p.*); Boucherville, and Boucherville, Ile du Large, both 1931, FF. Marie-Victorin & Rolland-Germain Nos. 43349 and 49343 (DAO, GH, *p.*). Labelle Co., Nominingue, 1932, E. Roy No. 2520 (DAO, *f.*). Hochelaga Co., Bout-de-l'Ile, 1932, FF. Marie-Victorin & Romain-Rolland No. 46805 (DAO, GH, *f.-p.*). Laval Co., Sainte-Rose, 1932, FF. Marie-Victorin & Romain-Rolland No. 46806 (GH, *p.*). Bellechasse Co., Saint-Vallier, 1932, F. Marie-Victorin *et al.* No. 44091 (GH, *h.*). Richelieu Co., Saint-Ours, 1932, FF. Marie-Victorin & Romain-Rolland No. 46248 (GH, *h.*); Sainte-Anne-de-Sorel, 1943, F. Marie-Victorin *et al.* No. 2256 (BM, DAO, *f.-p.*). Jacques-Cartier Co., Pointe-Claire, 1932, FF. Marie-Victorin & Romain-Rolland No. 46813 (GH,

h.). Abitibi region, L. Figuery, 1933, F. Marie-Victorin *et al.* No. 44992 (DAO, *f.*). Vaudreuil, Co. Rigaud, 1934, E. Roy No. 3197 (DAO *h.*). Lachine, 1936, H. Groh (DAO, *f.-p.*). Rimouski Co., Saint-Fabien, 1937, FF. Marie-Victorin & Romain-Rolland No. 49420 (GH, *f.-h.*). Sainte-Anne du Lac, 1938, H. Groh (DAO, *p.*). Hudson Bay, E. coast, Great Whale River, 1939, J. Marr No. 3984 (DAO, *p.*). Lake Roland, 100 km N. of Mont-Laurier, 1941, FF. Marie-Victorin & Romain-Rolland No. 306 (GH, *h.*). Napierville Co., Napierville, 1942, F. Marie-Victorin *et al.* No. 56033 (GH, *h.*). Brome Co., Sutton, 1942, F. Marie-Victorin *et al.* No. 56204 (GH, *f.*). Soulanges Co., Coteau-du-Lac, 1944, F. Marie-Victorin *et al.* No. 2351 (DAO, *h.*). Gatineau Co., Hull Twp, Leamy Lake, 1947, W. G. Dore & J. A. Calder No. 47–1116 (DAO, *p.*). Fort Chimo area, 1948, J. A. Calder No. 2344 (DAO, *p.*). Kamouraska Co., Ste-Anne-de-la-Pocatière, 1948, R. Paquin No. 365x (DAO, *f.-h.*). Papineau Co., Lochaber Twp, L. la Blanche, 1950, J. A. Calder & H. Rhodes No. 4868 (DAO, *h.*); Thurso, by Ottawa R., 1955, L. Jenkins No. 6456 (DAO, *h.*) and 1962, W. G. Dore No. 20142 (DAO, *h.-p.*). Champlain Co., St. Louis-de-Champlain, 1951, I. J. Bassett & A. Hamel No. 2016 (DAO, *f.*). Rouville Co., Mt. Yamaska, 1951, F. Fabius No. 5565 (DAO, *f.*). Québec Co., Sillery, 1951, R. Cayouette No. 51–231 (DAO, *p.*). J 1285. *Ontario:* 1876, Macoun No. 138 (K). London, 1879, Burgers (BM). Russell Co., Casselman, 1891, W. M. Scott (DAO, *h.*). Cataraqui Creek, 1893, I. K. McMorine (DAO, *h.*). Leamington, 1901, J. Macoun No. 33845 (GH, *f.*). Plevna, 1902, J. Fowler (GH, *f.-h.*). Algoma Distr., Pancake Bay, 1935, T. M. C. Taylor *et al.* No. 1955 (GH, *h.*). Thunder Bay Distr., Walker Lake, Schreiber, 1937, R. C. Hosie *et al.* No. 691 (GH, *p.*); Crooks Twp, Little Pigeon Bay and Pine River, both 1952, C. E. Garton, Nos. 1812 and 2053 (DAO, *f.*); Kilkenny Twp, Lake Nipigon, E. of Pijitawabik Bay, 1960, South Bay, 1960, and 5 km N. of MacDiarmid, 1961, all C. E. Garton Nos. 7529, 7818 and 8340 (DAO, *h.*, *p.*); Lake Nipigon, N.E. of Pijitawabik Bay, 1961, E. G. Voss No. 10255 (DAO, *h.*); White Lake, Government Bay, 1961, E. G. Voss No. 10490 (DAO, *h.*). Stormont Co., Cornwall Twp, Cornwall, 1939, H. W. Minshall No. 1287 (DAO, *h.*). Ottawa Distr., Ottawa, Central Exp. Farm, J. A. Guignard (DAO, *h.*); Carleton Co., Nepean Twp, Jock River, 1946, Senn *et al.* No. 4 (DAO, *h.*); Carleton Co., North Gower Twp, 1946, W. H. Minshall No. 338 (DAO, *f.-h.*); Ottawa South, Bronson dump, 1951, W. G. Dalzell & I. J. Bassett No. 47 (DAO, *h.*); Carleton Co., Blackburn, 1954, L. Jenkins No. 4838 (DAO, *h.*); Carleton Co., Nepean Twp Chartrand Isl., 1955, J. M. Gillett & K. M. Graham No. 9779 (DAO, *h.*). Lake Erie, Long Point, 1938, H. A. Senn & J. H. Soper No. 602 (DAO, *h.*). Longlac, 1946, H. Groh No. 3230 (DAO, *p.*). Elgin Co., Yarmouth Twp, St. Thomas, 1949, L. E. James No. 78 (DAO, *h.*); near St. Thomas, 1950, L. E. James (DAO, *h.*). Cochrane Distr., Timmins, 1950, I. J. Bassett & K. K. Bragg No. 1250 (DAO, *f.-h.*). Grenville Co., Prescott, 1953, W. G. Dore & J. M. Gillett No. 14889 (DAO, *f.-h.*). Dundas Co., E. of Iroquois, 1953, W. G. Dore & J. M. Gillett No. 14648 (DAO, *h.*); Aultsville, 1954, Dore & Van Rens No. 15682 (DAO, *f.-h.*). Lake Ontario, W. of Port Hope, Willow Beach, 1956, W. J. Cody *et al.* No. 9486 (DAO, *h.* $2n = 32$, Mulligan 1964). *Manitoba:* Red River, vicinity of Winnipeg, 1940, W. N. Denike No. 1414 (DAO, *f.-p.*). Riding Mountain Nat. Park, Clear Lake, 1941, E. Scamman No. 2893 (GH, *p.*). Near Ethelbert, 1946, J. H. Connors (DAO, *f.*). Woodnorth, 1947, R. H. Mooney (DAO, f.). Fort Churchill, gravel area, 1948, J. M. Gillett No. 2219 and 2532 (DAO, *p.*); border of lake, 1948, J. M. Gillett No. 2634 (DAO, *p.*). Near Winnipeg, Eastern Transcona Terminal, 1949, C. Frankton No. 1035 (DAO, *f.-p.*). Sasaginnigak Lake, 1949, A. J. Breitung No. 7703 (DAO, *p.*). Churchill Distr., Gillam, 1950, W. B. Schofield No. 1227 (DAO, DUL, BM, *p.*). Brandon, 1951 and 1958 G. Stevenson Nos. 400 and 1549 (DAO, *f.*). Reindeer Lake, 1951, W. K. W. Baldwin No. 2138 (GH, *f.*). Grassy Narrows, 1952, A. & D. Löve No. 5486 (DAO, *p.*); at L. Winnipeg, 1961, W. G. Dore No. 19487 (DAO, *p.*). Western James Bay Watershed, Albany, 1952, E. Lepage No. 30226 (DAO, *f.-h.*). Brokenhead, 1952, T. Mosquin

No. 155 (DAO, *f.*). Delta, 1953, A. & D. Löve No. 5820 (DAO, *f.*). The Pas, 1954, W. Krivda No. 1305, (DAO, *f.*). Brown, 1955, A. & D. Löve No. 6607 (DAO, *f.*). Souris Distr., Horton, 1957, I. J. Bassett & J. W. Kemp No. 3536 (DAO, *f.* $2n = 32$, Mulligan 1964). Assiniboine River, N.W. of Brandon, 1961, G. A. Mulligan No. 2644 (DAO, *f.*). W. of Brandon, 1961, G. A. Mulligan No. 2596 (DAO, *f.*). *North-West Territories, Mackenzie District:* Arctic coast between C. Barrow and Mackenzie R., 1849, Pullen No. 26 (K, *p.*). Hay River and Athabaska River, both 1928, R. R. Gates & K. Mellanby (K, *p.*). Wood Buffalo Park, Gov. Hay Camp Distr., Slave River, 1928, H. M. Raup No. 2506 (GH, *p.*); Near Hart (Raup) Lake, 1928, H. M. Raup No. 2501 (GH, *h.-p.*). Great Slave Lake, Gros Cap Isl., 1948, E. T. Reeder No. S 2895 (DAO, *f.-p.*). Salt River, 1950, W. J. Cody & C. C. Loan No. 4601 (DAO, *p.*). Little Buffalo River, W. of Ft. Smith, 1950, W. J. Cody & C. C. Loan No. 4735 (DAO, *f.-p.*). Port Radium, Eldorado Mine, 1949, W. J. Cody No. 2791 (DAO, *p.*). Lower Hay River, 1951, W. H. Lewis No. 726 (GH, *f.*). Norman Wells, 1953, W. J. Cody & R. L. Gutteridge No. 7335 and 7679 (DAO, *p.*). Fort Simpson, garden, Community Centre, and mainland S. of Ft. Simpson Isl., all 1955, W. J. Cody & J. M. Matte Nos. 8724, 8756 and 9090 (DAO, *f.-h.*); 1955, near Corps Signals Transmitters,W. J. Cody & J. M. Matte No. 9269 (DAO, *p.*). Eskimo Lakes, mouth of Sitidgi Creek, 1957, W. J. Cody & D. H. Ferguson No. 10765 (DAO, *p.*). Liard River, 30 and 13 km S.W. of Fort Liard, both 1961, W. J. Cody & K. W. Spicer Nos. 11528 and 11637 (DAO, *p.*). Mackenzie River–Yellowknife Highway, Mile 61.2 N and 5.7 S, both 1961, J. W. Thieret & R. J. Reich Nos. 7597 and 7807 (DAO, *f.*). J 1452, 1453.

Appendix 4. Nordic finds of *Rorippa sylvestris*

The Appendix lists at first hand herbarium specimens. Literature reports are referred to only in cases where no voucher specimens have been found, unless some essential circumstances about the find, not indicated on the label, have been published. Localities covered by one symbol in Fig. 13 or, for localities at L. Mälaren, Fig. 16, are grouped together within dashes. Only the oldest collections or those giving special information are referred to in detail from places where the species has been collected a great number of times. For further explanations see p. 167.

Denmark

Jylland: D. 27. Ribe, 1851, d'Origny (C). 1885, N. O. Thomsen (C). – D. 11. Hobro, harbour, 1878, Anon. (C); at fountain near harbour (without date), J. Mörch (C). – D. 24. Grumstrup, fen 1894, V. Österberg (C, *11*); K. Wiinstedt: Botanisk Tidsskrift 34, p. 146, 1917. – D. 24. Horsens, Bögelund, roadside, 1902, K. Wiinstedt (C, LD, UPS); Further loc. cf. Wiinstedt (op. cit.). – D. 25. Vingsted, 1905, N. J. Andersen (C); near railway station, 1912, C. H. Ostenfeld (C); mill, 1963, A. Hansen (C). – D. 20. Between Bryraf By and Kvirdsö, ditch, 1906, K. Wiinstedt (C). – D. 15. Feldborg nursery garden of forestry, 1906, H. Bojesen (C). – D. 13a. Hvallöse fen, 1908, H. Hammer (C). Alling To near Sjællebro, roadside, 1946, S. Andersen (C). Ölst, roadside, 1960, A. Hansen (C). – D. 25. Hejls-Vejstrup, roadside, 1911, A. Lange (C); 1927, K. Wiinstedt (C). – D. 26 and 27. Varde, ditch at Varde River, 1912, P. Larsen (C, *11*); 1927, T. Sörensen (C). – D. 27. Esbjerg, 1914, P. M. Pedersen (AAU, C, *11*). – D. 25. Kolding, 1914, M. P. Christiansen (C). – D. 18. Bording, at fen N.E. of railway station, 1914, P. Larsen (C). Ikast, 1929, Past-Höeg (C). – D. 9. Fur, fields, 1917, J. Gröntved (C); Engelst, 1937, J. Lindhard (C). – D. 7. Thy, Sjörring Sö, drained lake,

1917, C. H. Ostenfeld. – D. 4. Jydske Ås, Stagsted wood, Boller, 1919, K. Wiinstedt (C). N of Dronninglund forest, field (without date) A. Paulsen (C). – D. 52. Åbenrå, railway, 1921, C. H. Ostenfeld (C). – D. 50. Skart, field, 1921, Pedersen (C). – D. 11. Rostrup, meadows, 1922, A. Michelsen (C, *11*). – D. 52. Gråsten, on bridge, 1922, K. Wiinstedt (C). – D. 52. Kruså, Krusågård, 1923, C. H. Ostenfeld (C, *11*); ditch, 1925, H. P. Kristensen (C); roadside, 1929, K. Wiinstedt (C, *11*). Kollund, 1929, Lindhard (AAU). – D. 17. Söndervig, road, 1924, J. Grüner (C). – D. 13b, 14 and 21. Terp, at R. Nörre Å, 1924, A. Klinge (C). Fladbro, 1934, K. Wiinstedt (C). Langå, 1939, Anon. (C). V. Alling, at Alling River, 1965, E. Worsöe (C). Nymölle, watercourse, 1965, K. Larsen No. 21448 (AAU). – D. 17. Skern, 1926, Lindhard (AAU). – D. 24. Ölsted, railway station, 1929, K. Wiinstedt (C). – D. 14 and 20. Funder, Gröndalen, 1932, K. Wiinstedt (C). Silkeborg, path, 1945, Peterzon (C). – D. 22 b. At old Grenå River, 1935, K. Wiinstedt (C). – D. 4. Sæby, harbour, 1936, G. Degelius (S). – D. 9. Nyköbing M., waste place, 1941, Lindhard (AAU). – D. 14. Lövaskal, 1944, A. Schwarzer (C). Skern, Karmark mill, 1965 and St. Karmark wood, 1966, E. Worsöe (C). – D. 21. Århus, 1949, J. Mikkelsen (C); Viby, refuse place, 1960, H. Öllgaard (AAU). – D. 5. Fjerritslev, yard, 1950, S. Andersen (C). – D. 27. Henne, roadside, 1953, T. Sams (C). – D. 16 and 18. Holstebro, 1954, A. Jensen (C). Tvis, railway station, 1963, H. Ödum (C). – D. 5. Panderup, Albaksgård, at canal, 1958, A. Hansen (C, *11*). – D. 5. Brönderslev, Rebs meadows, at canal, 1958, A. Hansen (C, *11*). – D. 50. Hviding, railway station, 1959, E. Pedersen (C) and 1962, J 873 (*10*). – D. 14. Viborg, refuse place, 1960, L. Ingerslev (C). – D. 6. Hanherred, Slettestrand, at dunes, 1960, A. Hansen (C). – D. 2. Kjærsgård Strand, at R. Liverå, grassy ground, 1960, H. Lorentzen (C) and 1961, H. Transtedt (C). – D. 2. Hjörring, refuse place, 1961, H. Lorentzen (C); nursery garden, 1964, H. Lorentzen (C). – D. 26. 4 km W. of Grindsted, 1962, E. Jensen (C). – D. 1. Between Blæsbjerg and Elling, at ditch, 1965, H. Lorentzen (C). – D. 14. Near Bjærringbo, at stream, 1965, E. Worsöe (C). – D. 22a. Rodskov, 1966, E. Worsöe (C).

Als: D. 53. Hummelmai, 1849, Th. Schiötz (C) (is possibly a *R. amphibia* × *sylvestris* very close to the latter. Cf. A. Pedersen: Bot. Tidsskr. 54, p. 246, 1958). Tandslet and Österholm, both 1922, M. P. Christiansen (C).

Ærö: D. 33. Hornbæk meadows, ditch, 1942, A. Klinge (C). Skovby, Flintholmsgård, pond, 1966, A. Hansen (C).

Fyn: D. 32. Svendborg, waste place, 1912, F. Höen (C, *11*); cemetery, 1913, N. Sörensen (C). – D. 28. Assens, harbour, 1917, K. Wiinstedt (C, *11*). – D. 31. Nyborg, 1931, J. Grüner (C, *11*). – D. 29. Odense, harbour, 1933, C. Groversen (C, *11*) and 1939, Lindhard (AAU); 1944, H. Damgaard-Pedersen (C). – D. 31. Ringe, 1962, J. Pedersen (C). – D. 29. Bogense, 1963, A. Hansen (C). – D. 28. Middelfart, Skovgården, garden, 1965, A. Hansen (C).

Samsö: D. 23. Kalby Kås, roadside, 1939, S. Andersen (C).

Sjælland: D. 45a. Jonstrup, at L. Söndersöen, 1866, 1867, 1872, 1889, H. Mortensen (AAU, C, GB, S, UPS), 1869, P. Nielsen (C), 1879, F. Svendsen (LD), 1894, C. Ostenfeld-Hansen (C, *11*), 1890, P. Baagöe (C). Cf. H. Mortensen: Bot. Tidsskr. 2, p. 255, 1868. – D. 41. Korsör, Forlöv, at Vårby R., 1869, P. Nielsen (C). Cf. P. Nielsen: Bot. Tidsskr. 2. Række, 2, p. 366, 1874. – D. 46. Köbenhavn, Amager, Sundbyvester, moist refuse place, 1894, C. Ostenfeld-Hansen (C) and J. Hartz (C, *11*). Several coll. in Köbenhavn 1898–1964 (*11*). – D. 41. Næstved, Store Mylle, 1898, P. Baagöe (C). – D. 45b. Hilleröd, Stenholt, field, 1911, K. Ravnkilde (C, *11*). Nöddebo, grassy ground, 1911, K. Hansen (C). – D. 45a. Klampenborg, St. Andreas Kollegiet, garden, 1918, Breitung (C, *11*). Gentofte, refuse place, 1939 and 1941, S. Andersen (C); roadside, 1956, K. Larsen (LD); 1966, J 1545. Holte, market garden and roadsides, 1941, S. Andersen (C, *11*); 1962, J 886 (*10*). Springforbi, experimental garden, 1944, C. H. Bornebusch (C). Söborg, 1944, A. Vesterdal (C). Lyngby, gar-

den, 1960, K. Jensen (C). Avedöre, adventitiously, 1965, A. Hansen (C). – D. 45b. Helsingör, Lappen, "at least since 12 years", 1927, S. Andersen (C); 1922, Feilberg (C). – D. 45b. Frederikssund, garden, 1928, C. V. Lange (C); refuse place, 1938, S. Andersen (C); roadside, 1957, A. Hansen (C) and 1962, J 869 (*10*). – D. 45a. Jyllinge, at R. Harrestrup Å, 1944, M. Nielsen (C). – D. 41. Slagelse, refuse place, 1944, L. Ingerslev-Hansen (C); roadside, 1963, A. Hansen (C). – D. 43. Fårevejle, railway station, 1946, K. Wiinstedt (C); 1962, J 870 (*10*). – D. 45b. Frederiksværk, roadside, 1957, A. Hansen (C). – D. 45b. Smidstrup Strand, 1957, A. Hansen (C). – D. 41. (40?). Sorö, cemetery, 1957 (or Herfölge, 1956), E. Jensen (C).

Falster: D. 37. Stubbeköbing, 1851, A. Benzon (C). Skörringe, 1965, H. Petersen (C). – D. 37. Nyköbing, on bridge, 1868, K. P. Koch (C, UPS). Tingsted, 1925, C. A. Jörgensen (C). Stubberup, market garden, 1960, G. Dybkjær (C) and 1962, J 877 (*10*).

Lolland: D. 35. Höireby, 1847, E. Möller-Holst (C). Hillested, 1859, E. Rostrup (C). – D. 35. Rödby, 1848, E. Möller-Holst (C). Bjernes, near refuse place, 1936, S. M. Rasmussen (C). – D. 35. Nakskov, various places in town 1850–1885, E. Rostrup (C, LD, UPS); street, 1892, C. Ostenfeld-Hansen (C); harbour, 1959, L. Ingerslev (C) and 1962, J 878 (*10*). – D. 36. Nysted, street, 1892, C. Ostenfeld-Hansen (C) and 1900, A. Möller (C, S).

Bornholm: D. 47. Limensgade, at R. Læså, 1848, 1860, J. Lange (C, UPS); 1850, T. Jensen (C) and T. Schiötz (AAU). At R. Vase Å, 1854, T. Jensen (C). At R. Grödbyå, 1859, RTH (C, *11*). Poulsker, E. of Hunsömyre Mölle, 1859, N. H. Bergstedt (C). Öleå (J. Baagöe: Bot. Tidsskr. 1, p. 29, 1866). Bodilsker, Sandegård (J. Lange: Bot. Tidsskr. 2, p. 60, 1867). Between Åkirkeby and Bodilsker, 1890, herb. Lange (C). Pedersker, Slusgård, 1888, H. Möller (C). – D. 47. Nexö, Nörrebæk (J. Lange: op. cit.); L. Farske Sö, 1883, Klöcker (LD, S); 1895, J. Hartz (C, UPS) and J. Baagöe (C). Some more old Bornholmian coll. without precise locality.

Sweden

Skåne: Lund and between Örtofta and Vidarp (E. Rosén: Observationes botanicae, p. 33, 1749). Lund, 1820, E. Fries (UPS). Segeby (without date), herb. Hartman (UPS). Kävlinge (without date), herb. E. Fries (UPS). Between Lund and Höjebro "in agris limosis" (E. Fries: Flora Scanica, p. 65, 1835). V. Hoby, Bösmöllan at R. Kävlingeån, 1881, S. Murbeck (LD). Håstad, Vadmöllan at R. Kävlingeån, 1887, G. Andersson (S). Flackarp, Trolleberg (without date), Anon. (LD). – Malmö, Södervärn, road (Rosén: op. cit.); the harbour (N. Lilja: Skånes flora ed. 2, p. 462, 1870) and 1886, G. Johansson (BM). 5 more coll. in the town 1895–1930 (cf. S. Asker: Bot. Not. 112, p. 279, 1959). Alnarp, 1858, L. J. Wahlstedt (LD); garden, 1922, A. Nilsson (LD). Hyllie, "in pratis maritimis", 1900, O. Holmberg (BG, GB, S, UPS). Arlöv, 1923, 1928, R. v. Steijern (LD). Åkarp, garden, 1937, A. Berg v. Linde (LD, UPS, *11*). – Kristianstad, 1818, herb. Hartman (UPS); 1853, Westerlund (S); 1878, Zetterstedt (LD); Helge River, 1881, E. Ljungström (LD); 1887, Dusén (UPS, *11*); Långebro, 1889, G. Nilsson (GB), 1904–1909, Theorin & Hasslow (GB, LD, S, UPS); numerous adventitious coll. in and around the town up to present time. J 581 (*10*). – Landskrona (E. Fries: Fl. Scan., p. 65, 1835); gardens, 1945 and 1953, A. Nilsson (LD); J 1103 (*10*). Cf. A. Nilsson: Bot. Not. 1942, p. 201 and 1952, p. 85. – Vittskövle, at the ferry, 1850, Zetterstedt (LD); riverside, 1935, A. Torlöw (LD). – Broby, at Helge River, 1859, C. J. Hamnström (LD). – Billinge (F. W. C. Areschoug: Skånes Flora, p. 71, 1866). – Trelleborg, 1880, A. Magnusson (S), 1886, G. Andersson (LD, S). – Tygelsjö, Pile, sown meadow, 1886, E. Ljungström (LD); 1894, H. G. Simmons (UPS); ditch, 1894, C. Ostenfeld (C). – V. Karaby, Ålstorp, water-mill, 1886, N. Alvthin (LD). Saxtorp, Thorsgård, water-mill, 1892, N. Alvthin (LD); at R. Saxån, 1947, H. Emanuelsson (LD). – Brunnby, Mölle, 1890, N. Larsen (C); Kullen, 1892, Kjellberg (H) and ditch, 1896, S. Birger (S); Mölle, roadside, 1947, C. A. Torén (LD).

– Vomb, 1900, O. M. & A. Nordström (H, LD). At L. Vombsjön, 1910, G. Sjöstedt (LD), 1943, J. Linders (LD). Öved, 1959, H. Andersson (LD); J 1235, 1307. – Röddinge, Eriksdal, 1902, C. Kurck (LD). Lövestad (B. Sjöstedt: Bot. Not. 117, p. 91, 1964). – Hörby, 1911, A. E. Gorton (LD). – Revinge, Revingeby, 1923, C. Blom (GB, LD). – Båstad, Dala, 1927, A. G. Eliasson (S, UPS, *11*). – Hälsingborg, Stattena, ditch, 1936, S. Axell (LD, UPS); Leo factory, 1938 and Ramlösa, 1939, T. Lange (LD). – Ignaberga, S. of old church, 1942, H. Weimarck (LD, S); J 539 (*10*). – Andrarum, Ilstorp bridge, at stream, 1947, T. Hulthén (LD). – Andrarum, Buralycke, roadside, 1947, and Kristinehof, garden, 1947, T. Hulthén (LD). Eljaröd, Gumhusa, a pit, 1948 and Tjörneröd, a yard, 1948, M. Nilsson & T. Hulthén (GB, LD). – V. Karup, Faritslöv, garden, 1951, S. Selander (S). – Vitaby, adventitiously, 1959, H. Andersson (LD). – Höganäs, 1963, J 1108 (*10*). – [Reports in H. Vallin: Skånes Natur 32, p. 32, 1945 and A. Oredsson: Bot. Not. 114, p. 338, 1961 are doubtful.]

Blekinge: Karlshamn, at roads N.W. of the town (C. A. Gosselman: Blekinges flora, ed. 2, p. 117, 1865); 7 coll. in the town 1877–1934 (*11*). Mörrum, Vekerum (B. Holmgren: Blekinges flora, p. 171, 1942). – Asarum, Svängsta (K. B. Nordström: Bot. Not. 1891, p. 87). – Nättraby, Nerstorp, 1924, B. Holmgren (LD). Karlskrona, 1939, 1941, B. Holmgren (GB, LD, UPS, *11*). Further loc. in B. Holmgren (op. cit.). – Sölvesborg, 1931, harbour, 1932, 1939, B. Holmgren (GB, LD, UPS, *11*). – Ronneby, Kallinge, 1939, B. Holmgren (LD, S); near L. Härstorpsjön, garden, 1961, F. Lundberg (GB). Further loc. in B. Holmgren (op. cit.).

Småland (Sm and Klm): Ryssby, 1850, Westerlund (S); Ryssbylund, 1864, G. A. Tiselius (UPS, *11*); J 1234 (*10*). – Västervik, at the baths, 1854, A. Heinrici (GB), 1861, K. Vistrand (UPS); Strömsholmen, 1869, A. Lund (S). – Oskarshamn, 1880, C. Starbäck (S), 1886, Strohl (UPS), 1903, 1917, O. Köhler (GB, LD, S, UPS). – Kärda, Herrestad, 1888, O. Hagstrand (S). – Vrigstad, bridge, 1891, Lindegrén (S). – Almundsryd, Ålshult, railway station (C. T. Mörner: Bot. Not. 1914, p. 225); Ålshult, 1917, L. M. Neuman (LD). – Rogberga, Åkerby, at peat factory, 1919, K. Johansson (S); Tenhult, garden, 1941, F. Lundberg (GB). – Växjö, 1919, C. Pleijel (S), 1933, A. S. Trolander (LD). – Kalmar, 1924, H. Lenander (S); garden, 1935, R. Sterner (GB, LD, S); 1926, S. Torgård (LD); Fredriksskans, 1926, A. J. Snell (S, UPS, *11*); harbour and railway, 1942, T. Sundin (GB, LD). – Markaryd, 1927, T. Brandt (LD). – Jönköping, 1928, I. Lilja (LD, UPS, *11*). – Ljungby, Ljungbyholm, garden, 1936, C. M. Rydén (LD). – Marbäck, Herrestad, at dam, 1954, F. Hård av Segerstad (GB).

Öland: Högby, Horn and Vedby (G. Sjöstrand: Bot. Not. 1850, p. 243 and N. Acta Soc. Scient. Ups. 14, p. 484, 1850); Horn, 1914, O. Köhler (S) and 1922, T. Thorné (LD, S, UPS); Horn, and Dödevi, pits at roadside, and Gudesjölund, roadside, all 1932 (R. Sterner: Acta Phytogeogr. Suec. 9, p. 107, 1938). – Böda, 1862, 1879, O. Vesterlund (S, TURA). – Köping, Rosenfors, "in fossis" (G. Sjöstrand: N. Acta Soc. Scient. Ups. 14, p. 484, 1850, as *Nasturtium anceps*); Rosenfors, 1888, G. Lunder (LD, UPS). Borgholm, 1862, Westerlund (S); brook, 1893, K. F. Dusén (S), 1911, T. Erdmann (S), 1912, A. L. Segerström (S); 12 more coll. 1885–1911. – Kastlösa, 1882, E. Petersson (GB). – Högsrum, Vedby, road, 1936 (R. Sterner: Acta Phytogeogr. Suec. 9, p. 107, 1938), 1962, J 913 (*10*). – Glömminge, Ryd, brook, 1933, R. Sterner (S). – Mörbylånga, near the harbour, 1948, C. G. Alm No. 1068 (UPS).

Gotland: At roads in several places (without date), herb. Wahlenberg (UPS), and Hartman (UPS). – Hellvi, Malms, "in fossis ad viam" (G. Wahlenberg: N. Acta Soc. Scient. Ups. 8, 1821, as *Sisymbrium anceps*). – Källunge (Wahlenberg: op. cit., as *S. anceps*). – Fardhem (Wahlenberg: op. cit., as *S. anceps*). – Grötlingbo (Wahlenberg: op. cit., as *S. anceps*); quarry, 1894, K. Johansson (UPS); Sallmunds, 1940, E. T. Fries (LD, S, UPS, *11*). – Roma, 1830, C. Säve (S). – Visby, harbour (C. Säve: Synopsis Florae Gothlandicae, p. 22, 1837); the

harbour, 1860, T. O. B. N. Krok (UPS); numerous coll. 1863–1962; J 912 (*10*). – Rone, "in pratis", 1841, J. W. Zetterstedt (LD); 1907, E. T. Fries (S). – Hemse, Gannsarve, 1852, N. C. Kindberg (UPS). Alva (K. Johansson: K. Sv. Vet. akad. handl. 29:1, p. 177, 1897). – Dalhem, Duna, 1852, O. A. Westöö (GB); at R. Dalhemsån, 1909, T. Tengvall (S), 1911, E. T. Fries (GB, S). Hörsne, at the river (K. Johansson: op. cit.); J 900 (*10*). – Klintehamn, 1858, L. F. Nilsson (GB), 1873, K. F. Thedenius (UPS, *11*); ship-yard, 1896, C. Tillman (S); pier, 1898, K. Johansson (UPS, *11*); 1909, T. Tengvall (UPSV). – Slite, 1872 (J. E. Zetterstedt: Bot. Not. 1874, p. 165); beach, 1902, K. Johansson (UPS, *11*); harbour, 1925, A. Lindegrén (S); 6 more coll. 1904–1927 (*11*). Othem, 1895, E. v. Feilitzen (UPS, *11*); ditches, 1896, M. Östman (S). – Lärbro, 1872, S. A. Smedberg (UPS); Storugns, 1885, Anon. (S). – Östergarn, Katthammarsvik, 1879, C. Lindman (S), 1910, K. Johansson (S), 1932, E. T. Fries (GB, LD, S, UPS, *11*); (K. Johansson: op. cit.). – Lokrume, Hammars (K. Johansson: op. cit.). – Lummelunda (K. Johansson: op. cit.).

Östergötland: Kimstad, 1888, Haglund (S, UPS). – Kaga, 1861, 1864, E. K. Kastensson (GB, LD, UPS); 1864, R. Ygberg (LD) and A. Lindeberg (BG, UPS); Nybro, 1869, N. C. Kindberg (UPS); 1962, J 620 (*10*). Vreta kloster, at L. Roxen, 1867, B. Rudling (LD, UPS, *11*); Nybro, 1868, T. Neuman (O), and 1869, N. C. Kindberg (UPS, *11*). Berg, 1869, N. C. Kindberg (UPS); Linköping, Säby, 1882, N. C. Kindberg (UPS); Nykvarn (without date), Wallman (S). Rystad, at L. Roxen (N. C. Kindberg: Östgöta flora, ed. 2, p. 199, 1874). – Norrköping (without date but before 1875), Anon. (LD); near the harbour, 1910, P. A. Issén (LD); ballast place (E. Genberg: Sv. Bot. Tidskr. 57, p. 362, 1963). Dagsberg, Djurö mill (E. Genberg: op. cit.). – Tåby, Mem, shore, 1882, H. v. Delwig (LD, S, UPS, *11*). – Kullerstad, Skärblacka, lawn, 1930, N. Hylander (S). – Svanshals, at R. Renstadsån near L. Tåkern, 1948, H. Smith Nos. 550 and 551 (UPS), 1960, J 185. – Krokek, Bränntorp (E. Genberg: Sv. Bot. Tidskr. 45, p. 136, 1951). – [Unverified localities in Kindberg's Östgöta flora are not included.]

Västergötland (except Gbg): Herrljunga, 1909, A. S. Trolander (LD, S). – Borås, park, 1914 (C. Sandberg & I. Söderberg: Sv. Bot. Tidskr. 16, p. 239, 1922); at R. Viskan, 1954, G. A. Westfeldt (GB). Sandhult, Sandered, Viken, 1914 and 1917 (Sandberg & Söderberg: op. cit.). – Ulricehamn, 1920, railway station (G. A. Westfeldt: Sv. Bot. Tidskr. 48, p. 727, 1954); 1922, G. A. Westfeldt (LD, S); railway, 1948, Ö. Nilsson (LD). – Fänneslunda, 1925 (G. A. Westfeldt: op. cit.). – Lerum, Ekebacken, waste place, 1927, F. Lundberg (GB); Hulan, garden, 1946, R. Ohlsén (S, UPS). – Skepplanda, Högstorp, near road, 1933, J. A. O. Skårman (S, UPS) and Sv. Bot. Tidskr. 29, p. 475, 1935. – Hillared, near church, weed, 1934, G. A. Westfeldt (S). – Finnekumla, Fästeredssund, 1934 (G. A. Westfeldt: op. cit.), 1952, G. A. Westfeldt (GB). – Alingsås, Kullingsberg, garden, 1938, R. Ohlsén (S). – Skövde, 1943, A. Hülphers (S, UPS, *11*). – Vänersborg, Skräcklan, compost, 1950, F. Lundberg (GB). – Angered, Lerjeholm (H. Fries: Acta Horti Gothoburg. 10, p. 77, 1935). Nödinge, Bohus, railway station, 1950, C. Blom (S) and H. Fries (GB), ship-yard, 1955, C. Blom (GB). – Töreboda, and Björketorp, near church (K. Hasselrot: Västergötlands flora, p. 99, 1967); not mapped.

Halland: Halmstad, ballast (without date), P. v. Friesen (UPS); park, 1909, 1910, F. Ahlfvengren (GB, S); 1930, J. Wiger (GB, S, UPS). – Gunnarp, at L. Fegen, 1911, F. Ahlfvengren (S). – Tvåker (F. Ahlfvengren: Hallands växter, p. 105, 1924). Sibbarp, Stegared, 1925, S. Svensson (LD). – Släp, Ramshult, garden, 1952, F. Lundberg (GB). – Laholm, Altona, garden, 1952, F. Lundberg (GB) and roadside, 1963, J 1109 (*10*). – Morup, Morupstånge, 1960, E. Carlsson (GB). – Fjärås, Tjolöholm, grass slope, 1960, Ö. Nilsson (LD) and 1964, M. Ohlander (GB).

Göteborg region (Gbg): Göteborg (O. Bromelius: Chloris gothica, 1694); "ad ripam amnis

Mölndalsån" (J. E. Areschoug: Plantae Cotyled. Florae Gothoburg., p. 54, 1836), 1837, Liebmann (C); streets, 1856, A. Benzon (C); near Haga church, 1860, G. L-d (LD); Pustervik, 1861, E. A. Trana (GB) and 1862, O. Landgren (GB). Numerous coll. in and near the city 1895–1962 (*11*); J 890 (*10*). – Råda, Mölnlycke, 1891, A. Uhlemann (LD), and 1946, H. Fries (GB, S). Mölndal, Lagklarebäck, 1940, H. Fries (GB, LD, S, UPS, *11*); 1944, H. Fries (GB, S); Kikås, near cemetery, 1953, C. Blom (GB); Landvetter, Salmered, 1924, H. Fries (GB); church village, 1926, T. Borgvall (GB) Askim, Billdal, 1934, H. Fries (GB) – Öckerö, Kalvsund, 1894, K. L. Larsén (GB, LD, S, UPS), 1903, J. E. Palmér (LD).

Bohuslän (except part of Gbg): [Bahusia (without date) Düben (UPS).] – Skaftö, near Fiskebäckskil, 1920, T. Arwidsson (S); Fiskebäckskil, 1930, H. Fries (GB, S). – Foss, Lycke, 1929, J. E. Palmér (GB, LD); Munkedal, roadside, 1933, H. Fries (GB, S). – Norum, at church, 1930, H. Fries (GB, S); Stenungsund, garden, 1963, F. Lundberg (GB). – Kville, Fläskön outside Fjällbacka, probably introduced with soil, 1943, T. Svedberg (UPS). – Ödsmål, Ribbetegen, potato field, 1945, and Hällsbacken 1947, E. Almqvist (GB); Hällesdalen, road, 1956, M. Ohlander (GB). – Kungshamn, Hasselö, 1947 (C. Blom: Acta Horti Gothoburg. 24, p. 97, 1961). – Strömstad, Tången, moist bank, 1950, K. Bökman (GB). – Harestad, Sjöhed, 1951, H. Fries (GB, S). – Uddevalla, Ardmore, garden, 1953, H. Fries (GB). – Resteröd, Ranneberg, garden, 1955, F. Lundberg (GB) and 1963, J 963.

Dalsland: Steneby, Baldersnäs, 1884, Wittrock (S). – Fröskog, Strand mine, roadside, 1927, F. Hård av Segerstad (GB). – Skållerud, Åsensbruk railway stn., 1962, E. Almquist (UPS).

Värmland: Karlstad, 1932, R. Ohlsén (GB, S), 1934, E. Kjellgren (LD, UPS, *11*). Cf. E. Almquist: Sv. Bot. Tidskr. 57, p. 173, 1963. – Karlskoga, Rävåsen, garden, 1938, T. Rydén (S). – Hagfors, railway, 1943, F. Hård av Segerstad (GB, S). – Köla, Växvik, roadside, 1943, E. Almquist (UPS). – Arvika, 1943, E. Kjellgren (LD). Cf. E. Almquist (op. cit.). – Rämen, lake shore at Rämmen, 1945, F. Hård av Segerstad (GB).

Närke: Götlunda, Humlemyrsviken, 1858, O. G. Blomberg (LD) and 1891, M. Victorin (LD, UPS); at bay between Locknäs and Hästnäs, 1858, 1864, 1888, O. G. Blomberg (LD, UPS). – Gällersta, Almbro, at stream, 1901, T. Svedberg (UPS). – Lillkyrka, Ekeberg, 1954, C. G. Alm No. 2229 (UPS).

Södermanland (except part of Stockholm): Localities outside L. Mälaren: Öja, at L. Hjälmaren, 1884, W. Blomberg (UPS, *11*). Julita, Hjälmaresund, 1894, E. Tegnér (O, S). – Nyköping, Örstigsnäs (H. Samzelius: Bot. Not. 1884, p. 146). – Eskilstuna, Tunafors, 1902, E. Andersson (GB); garden, 1949, E. Almquist (UPS). – Saltsjöbaden, 1912 (E. Almquist & E. Asplund: Stockholmstraktens växter, p. 224, 1937). Nacka, Jästängen, 1917, V. Laurent (S); Villa Plania, 1919, T. Vestergren (S); Lillängen, 1942, I. Björling (LD); Ektorp, waste place, 1943, B. Möllerström (LD); Saltsjö-Duvnäs, shore, 1947, H. Eriksson (S). – Västerhaninge, Fors, at stream near bridge, 1933, E. Asplund (S). – Oxelösund, 1960, J 171 (*10*). – Nynäshamn, Stockbonäs, waste place, 1965, E. Asplund (S).

Localities at L. Mälaren and some connected waters: Vallby and Sundby, 1841, M. A. Lindblad (S). Vallby, 1962, J 918 (*10*, *17*). – Strängnäs, Djäkneholm, 1846, K. J. Lönnroth (UPS); Nabbviken, 1846, herb. Zetterstedt (UPS); Visholmen, 1888 E. Köhler (GB, O, UPS, *11*), and 1889, A. Moberg (GB, O); 1920, Samuelsson: Pl. Suec. exs. No. 905. Several more coll., but none after 1920. – Västertälje, Kiholm, 1859, O. Tamm (S). – Botkyrka, at L. Tullingesjön, 1861, Crusebjörn (S; not in Fig. 16). – Jäder, Fiholm, 1862, U. Walmstedt (LD). – Södertälje, 1866, 1872, C. Lindblom (LD, S). – Toresund, Räfsnäs, 1873, R. Hult (H). – Sundby, Sundbyholm, 1876, F. Elmqvist (LD, UPS) and 1898, F. Ridderstolpe (S). – Överenhörna, Hamnskär, 1892, O. Hagström (S) and G. Fant (S); – Horn, 1893, V. Strandberg (S); – Ridön, 1893, V. Strandberg (S). – Aspö, Duvud, 1902, J. G. Laurell (S). –

Barva, 1906, C. & S. Cederblad (LD). – Botkyrka, Fittja, and Huddinge, 1931, F. Nilsson (GB, LD, UPS); Vårby (E. Almquist & E. Asplund: Stockholmstraktens växter, p. 224, 1937). – Ytterenhörna, Lövsta tegelbruk; – Sandviken (both Almquist & Asplund: op. cit.). – Helgarö, 1965, J 1388 (*10*, *17*). – Ytterselö, Äleby (C.-J. Clemedson: Selaön, Sörml. Handl. 22, p. 114, 1965).

Stockholm: Localities at L. Mälaren and some connected waters: "Prope Lazarettet", 1818, Hartman (UPS). Hammarbysjö, 1829, Anon. (S). Hornstull, 1838, J. O. Pontén (GB). Liljeholmen, 1846, N. & C. Lagerheim (S). Karlberg, 1852, S. O. Lindberg (S), numerous coll., latest 1929, (*11*). Tranebergsbro, 1858, J. Lagerheim (LD, S), 1904, H. & A. Fries (S); L. Ulvsundasjön, 1916, T. Erdmann (Samuelsson: Pl. Suec. exs. No. 906, *11*). Långholmen, 1860, Anon. (UPS). Marieberg, 1866, A. Thedenius (S). L. Essingen, 1869, H. Krook (S). Skanstull, 1873, O. Sternvall (LD). Årstaviken, 1878, Krok (S). Numerous more coll. but none after the 1920-ies (*11*).

Localities not at L. Mälaren: Årsta, ditch, (N. Lundequist: Flora paroecia Brännkyrka, p. 36, 1827). – Lill-jans, 1863, H. R. Hamberg (S). Värtan, 1901, H. Ström (S). – Djurgården, 1912, A. L. Segerström. Several adventitious coll. 1913–1965. J 1082 (*10*), J 1243 (*10*).

Uppland (except part of Stockholm): Localities at L. Mälaren and some connected waters: Sigtuna, the Steninge bridge, 1807, A. Areschoug (UPS), 1882, M. Floderus (UPS). – Skokloster, near church, 1820, and 1827, herb. Wahlenberg (UPS). – Håtuna, Signildsberg, 1862, Th. M. Fries (UPS, *11*). – Solna, Lilla Alby, 1864, C. M. Sondén (S). – Lossa, 1866, E. J. Widmark (S). – Enköping, 1869, 1871, 1873, L. J. Collén (S, LD, UPS, *11*); 1872, Thorsén (S) and A. N. Afzelius (UPS, TURA). – Uppsala, Hartman (O); R. Fyris, 1873, F. Ahlberg (GB); [1867, K. F. Thedenius, see p. 124]. – Torsvi, Brandholmssund, 1881, K. J. Haeggblom (LD, S, UPS). – Hilleshög, Bredlöt, 1891, F. Lundberg (S); Hilleshögviken, 1893, C. Reuterman (GB); – Near Sundsudd, 1892, C. Reuterman (GB). – A number of loc. in Adelsö Färentuna, Munsö, Sånga (Stockholmstraktens växter, p. 128, 1914). – Norrsunda, Rosersberg, 1912, E. Almquist (S). – Lovö, Drottningholm, 1914, E. Nordström (GB), 1916, A. L. Segerström (LD, S), 1920, F. Nilsson (GB, S), at canal, 1919, T. Vestergren (S). – Järfälla, Lövsta, 1915, A. L. Segerström (UPS); cf. E. Almquist & E. Asplund: Stockholmstraktens växter, p. 224, 1937. – Hilleshög, Riksätra, 1915, A. L. Segerström (S). – Sånga, Nibblenäs, 1915, A. L. Segerström (S). – Ekerö, Kersgatan, 1920, N. Bergvall (GB); – Skytteholm, 1935, J. Knöppel (S). – Munsö, Österås, 1962, J 929 (*10*, *17*). – Arnö, Oknö, 1962, J 892 (*10*, *17*).

Localities not at L. Mälaren: Solna, L. Brunnsviken and Lidingö, Mölnaträsk (K. F. Thedenius: Bot. Not. 1850, p. 80). Solna, Bergshamra (K. F. Thedenius, Botaniska exkursioner i Stockholmstrakten, p. 80, 1859). Lidingö, near church, 1890-ies (Almquist & Asplund: op. cit.). Sundbyberg, 1879, K. F. Thedenius (S) and 1916, T. Erdmann (GB, UPS, UPSV). Järfälla, Råcksta, L. Säbysjön, 1931, E. Almquist (S). Solna, 1963, J 1083 (*10*). – Skogstibble, 1870, S. Almquist (S); Ingla bridge, 1870-ies (E. Almquist: Flora upsaliensis, p. 158, 1965). – Älvkarleby, Skutskär, 1878, H. Thedenius (S), potato field, 1915, E. Almquist (UPS). Cf. Gstr: Valbo. – Färentuna, Kungsberga, adventitiously, 1925 (Almquist & Asplund: op. cit.). – Norrtälje, adventitiously, 1930–1934 (Almquist & Asplund: op. cit.); harbour, 1957, H. Smith No. 3249 (UPS), 1961, J 401 (*10*). – Uppsala, Lugnet, nursery garden, 1934 and later (E. Almquist: op. cit.); gardens, 1944, C. G. Alm No. 774 (UPS, *11*), 1960, J 357, 1961, J 531 (*10*), 1964, J 1254 (*10*). Vaksala, Fridhem, waste place, 1962, N. Lundqvist (UPS), 1963, J 960 (*10*).

Västmanland: Localities at L. Mälaren: Kolbäck, Strömsholm, 1819, Rosén (UPS). – Västerås, 1844, herb. Hartman (UPS), 1854, Kindberg (UPS); R. Lillån, 1891, 1892, D. Danielsson (S); harbour, 1925, O. Ohlin (GB) and 1931, L. Lindquist (GB); 1962, J 891 (*10*, *17*). –

Rytterne, Fiholm, 1848, herb. Cederstråhle (S). – Kungs-Barkarö, Örsåsen, 1848, K. J. Lönnroth (UPS). – Ängsö, Ängsösundet, 1873, A. N. Afzelius (LD, UPS), 1886, 1889, J. Agéli (S). – Rytterne, Tidö, 1876, F. Elmqvist (UPS). – Badelunda, Björnön, 1878, N. A. Johansson (LD), 1960, J 361 (*10*, *17*). – Västerås-Barkarö, Askö, 1882, E. Hemmendorff (S). – Kärrbo, Frösåker, 1885, J. Agéli (S). – Kungsåra, 1885, J. Agéli (S). – Kungsör, 1886–1888, C. O. v. Porat (GB, LD, S, UPS). – Lundby, Johannisberg, 1894, H. E. Johansson (S). – Rytterne, Hornsund, 1907 (G. Samuelsson: Sv. Bot. Tidskr. 17, p. 446, 1923); – Nyckelön, Kvicksund, 1910, T. Krok (S); Nyckelön, 1913, G. Lindmark (GB), 1960, J 186 (*10*, *17*). – Västerås-Barkarö, Almö-Lindö, 1920 (Samuelsson: op. cit.); – Skåpholmen, 1921, O. Ohlin (GB). – Kolbäck, Sävholmen. – Köping, Malmön (both: Samuelsson: op. cit.). – Rytterne, N. of Mellansundet, 1962, J 916 (*10*, *17*).

Localities not at L. Mälaren: Linde, 1865 (Samuelsson: op. cit.), at lake, 1873, O. Hamnström (LD); 1901, G. A. Ringselle (GB, LD, S, UPS). – Munktorp, near church, Kolbäck, Yllesta and Sörstafors (J. E. Iverus: Beskrifning öfver Västmanlands fanerogamer och thallogamer, p. 201, 1877). – Arboga, 1886, C. A. Tärnlund (GB); Viby, 1886, A. Larsson (UPS). – Sala, 1898, G. Dahl (S).

Dalarne: Falun, 1880-ies and later (E. Almquist: Dalarnes flora, p. 267, 1949). – Sundborn (Almquist: op. cit.). – Mora, Morastrand, lawn, 1911 (Almquist: op. cit.). – Älvdalen, Ö. Myckeläng, 1912, (Almquist: op. cit.). – Leksand, Noret, 1921–1926 (Almquist: op. cit.), 1962, J 602 (*10*). – Avesta, 1925 and later (Almquist: op. cit.). – Borlänge, Domnarvet, 1945 (Almquist: op. cit.). – Grangärde, Nyhammar, 1946, E. Almquist (S). – Ludvika, ruderal place, 1954, G. Björkman (LD, S, UPS, *11*) and R. Berglund (LD).

Gästrikland: Gävle, Bråbänk, 1832–1835, Anon. (UPS), 1835, Thedenius (LD); Holmsund, 1837, herb. Hartman (UPS, *11*), "copiose prope viam" 1847, Hartman (UPS); ballast place, 1849, herb. Lange (C). Several more coll. 1863–1939 (*11*). – Hille, Sätra, before 1891 (H. W. Arnell: Sv. Bot. Tidskr. 18, p. 111, 1924). – Valbo, Harnäs, 1857 (E. Almquist: Acta Phytogeogr. Suec. 1, p. 548, 1929); Arnell (op. cit., p. 111). Cf. Upl.: Älvkarleby.

Hälsingland: Hudiksvall, L. Håstaholmen, 1880, A. Berg (LD). – Söderhamn, 1891, I. Collijn (UPS, *11*). – Ljusdal, L. Borrsjön, 1919, 1935, G. Lidman (GB, UPS), 1934, G. Lidman (Samuelsson: Pl. Suec. exs. No. 907), 1963, J 1076 (*10*). – [Localities in Wiström: Förteckning öfv. Hälsinglands fanerogamer..., 1898, are not included.]

Medelpad: Skön, Kosta, 1877, K. A. T. Seth (LD, S, UPS). Timrå, 1879, C. F. Sundberg (S); Vivstavarv, ballast, 1885, J. A. Holm (LD). Sundsvall, market place, 1895, J. P. Linde (S). Several more coll. from this region 1885–1957 (*11*).

Ångermanland: Nyland, ballast (R. F. Fristedt: Växtgeografisk skildring af Södra Ångermanland, p. 23, 1857). – Härnösand, garden, 1922, N. Johnsson (GB, LD, S, UPS, *11*), cf. Lange: Sv. Bot. Tidskr. 20, p. 409, 1926; Kanaludden, 1952, K. Holm (LD); Kvarnholmen, harbour, 1960, E. Evers (LD); 1960, J 143 (*10*). – Själevad, Hörneborg sawmill, 1922 (G. Haglund: Bot. Not. 1923, p. 395).

Jämtland: Ås, Hållskaven, 1940, L. Strindberg (GB, S).

Västerbotten: Skellefteå, Strömsön, 1937, G. Cedergren (S), brewery, 1938, S. Nordenstam (S, UPS, *11*). – Umeå, 1967, J 1593 (not mapped). – [Localities in N. L. Andersson: Bot. Not. 1890, p. 36 not included.]

Norrbotten: Luleå, garden, 1960, J 188 (*10*).

Åsele Lappmark: Vilhelmina, Laxbäcken, garden, 1950, I. Svensson (S).

Lycksele Lappmark: Stensele, railway station, square garden, 1962, E. Almquist (UPS).

Pite Lappmark: Arjeplog, garden, 1930–1934 (C. T. Mörner: Bot. Not. 1935, p. 267), 1937, G. Wistrand (S).

NORWAY

Östfold: Moss, 1882, F. HOCH (O); 1894, A. BLYTT (O); park, 1962, J 859 (*10*). Jelöy, 1896, A. BLYTT (O), 1902, B. LYNGE (BG); 1906, J. HVERVEN (O); Krossern, 1946, K. ANDREASSEN (O). – Fredrikstad, 1889, K. PETERSEN (O); Kråkerö, ballast, 1904, H. JOHNSEN (LD, O); 1919, R. TAMBS LYCHE (TRH); Kråkerö, 1955, F. LUNDBERG (GB). – Sarpsborg, Sandesund, 1896, K. PETTERSEN (O); Greåker, 1961, K. ANDREASSEN (O) and 1962, J 860 (*10*). – Rakkestad, Bergenhus, cemetery, 1962 (appeared after 1960); Rolfseidet, 1962, both K. ANDREASSEN (O).

Akershus: Oslo, at R. Loenelv, Ellestad, 1834, BLYTT (O) and Kværner (N. LUND: Haandbog i Christianias phanerogame Flora, p. 131, 1846), "in ripis sabulosis", 1848 and later, M. N. BLYTT (BG, O, S, UPS). Several more coll. at R. Loenelv, the latest from the 1880-ies. – Oslo, ballast, 1882, KAALAAS (BG); Filipstad, 1885, R. E. FRIDTZ (GB, O), 1885, 1888, O. DAHL (O, TRH); Park at Royal Castle, 1900, T. HANNAAS (BG, UPS) and later, e.g. J 858 (*10*). Numerous more coll. in and around the city 1889–1964. J 865, 1069, 1070 (*10*), 1221 (*10*). – Bærum, road, 1891, 1892, O. DAHL (O), artificial meadow, 1932, P. STÖRMER (O). Asker, Hvalstad, 1916, (T. VESTERGREN: Sv. Bot. Tidskr. 10, p. 286, 1916), 1928, J. HOLMBOE (O, TRH), 1930, O. AALEN (O), and A. ARRHENIUS (O), 1938, F. LUNDBERG (GB); Holmen, 1957, P. SUNDING (O). – Ås, Agric. highschool, garden, 1926, J. LID (O), 1929, A. RÖSKELAND (O); 1940, H. B. GJÆRUM (O). Vestby, Ramme, 1958, P. STÖRMER (O). – Eidsvoll, Smedstuen, 1934, T. STORM (O). – Dröbak, 1942, J. LID (O). – Skedsmo, Strömmen, 1950, A. HÖGEVOLD (BG, O), 1956, K. ANDREASSEN (O).

Hedmark: Hamar, garden, 1883, J. RUD (O); 1891, G. JYNGE (BG), 1896, N. HVOSLEF (TRH); Ny Sagatun, 1896, A. LANDMARK (O). – Löten, railway station, 1938, O. HANSSEN (O).

Oppland: Fåberg, Nordre Ål, 1939, H. SATREN (O); cemetery, 1950 and 1955, O. JÖRSTAD (O), refuse place, 1956, O. JÖRSTAD (O). – Lunner, Mylla, at cottage, 1951, K. HYGEN (O).

Buskerud: Hole, road, 1881, F. HOCH (O). – Övre Eiker, Fiskum, Hailand, 1937, A. RÖSKELAND (O). – Modum, Geithus, 1948, P. STÖRMER (O).

Vestfold: Holmestrand, roadside at garden, 1903 and 1917, J. DYRING (BG, GB, O, S, UPS; cf. J. DYRING: Nyt Mag. Naturvidensk. 59, p. 111, 1921); 1912, C. LEEGAARD (O). – Svelvik, 1913, T. RUUD (BG). – Tönsberg, 1920, A. MAGNUS (O). – Sande, Galleberg, 1923, H. RESVOLL-HOLMSEN (O).

Telemark: Kragerö, Tallakshavn (ballast place), 1857, A. BLYTT (O); without dates, W. BOECK (O) and K. KRISTIANSEN (O). – Skien, street, 1887, A. LANDMARK (O); Skotland, 1887, J. DYRING (BG, O); 1896, T. RESVOLL (O); refuse place, and roadside, 1959, O. SVENDSEN (O). Gjerpen, Böle (silo), 1905, H. JOHNSEN (O). – Tinn, Rjukan, 1930, B. SJÖTVEIT (O). – Fyresdal, Moland, roadside, 1936, P. STÖRMER (O). – Holla, Holden, park, 1949, P. STÖRMER (O); Ulefoss, field, 1948, T. SKARD (O); 1960, K. ANDREASSEN (O). – Drangedal, near railway station, 1951, F. WISCHMANN (O).

Aust-Agder: Grimstad, Fevig, ship-yard, 1890, A. ARBO (O). – Hornnes, Krossen, roadside, 1943, A. DANIELSEN (BG, O). – Åmli, church village, 1950, P. STÖRMER (O). – Vegårshei, Myra, 1951, J. KAASA (O). – Froland, Frolands verk, 1953, J. KAASA (O).

Vest-Agder: Mandal, 1861, V. WITTROCK (S), on ballast and at sawmill, 1875 and later, R. E. FRIDTZ (O); 1884, S. MURBECK (LD, S, UPS), 1908, H. PRINTZ (TRH). Cf. R. E. FRIDTZ: Undersögelser paa kysten af Lister og Mandals amt, p. 158, 1903. – Flekkefjord, without date but before 1876, M. N. BLYTT (O). – Kristiansand, 1912, H. BENESTAD (O). Oddernes, Strai, field, 1959, A. BJÖRNDAL (O). – Lista, Vanse, Kjörrefjord, nursery-garden, 1916, A. GROSTÖL (O).

Rogaland: Hetland, Hillevåg, 1888, TENGELSEN (BG); Madla, Madlamoen, Leiren, 1951,

O. Rönning (BG). – Klepp, Lensmanslunden, 1890, O. A. Hoffstad (O); Sandnes, 1904, O. Dahl (O), and 1942, G. Jynge (BG); Sandnes nursery-garden, 1923, J. Lid (O); Höyland, 1931, A. Röskeland (O); Bryne, 1943, G. Jynge (BG). – Stangaland, Kopervik, garden, 1930, V. Rosseland (BG, O, TRH). Haugesund, Skeisvand, 1940, Y. Mejland (O). – Heskestad, at L. Gyavannet, 1938, I. & P. Störmer (O).

Hordaland: Bergen, 1871, Wulfsberg (O); at the museum, 1873, J. Greve (O); Sydneshaugen, 1874 and 1879, Crawfurd (BG); Möllendal, 1879, Brunchorst (BG) and later; nursery-garden, 1909, J. Holmboe (BG); Hæggernes mill, 1911, J. Holmboe (O) and 1930, Bödtker (O). Several more coll. 1875–1930. – Granvin, at L. Granvinsvannet, 1890 and later, S. K. Selland (BG, O, TRH, Herb. norv. Fridtz No. 31058); several more coll. 1895–1910; 1943, A. Aksnes (BG, O). Cf. S. K. Selland: Hardangerområdets flora, p. 100, 1920. – Voss, near Vossevangen, 1904 (S. K. Selland: Nyt Mag. Naturvidensk. 44, p. 192, 1906). – Kvam, Vikör, Aksnes, garden, 1908, S. K. Selland (BG); between Vikör and Framnes, 1944, M. Lillefosse (O). – Strandebarm, Lillefosse, Kalveskår, intentionally introduced, 1908, T. Lillefosse (BG); Tangerås, introduced, 1916 and 1929, T. Lillefosse (O); Röen, 1933, A. Röen (O); Bergsfjæren, 1941 and 1943, T. Lillefosse (BG, O). – Odda, Eid, with planted trees, 1909, S. K. Selland (BG); at factories, 1913 and later, S. K. Selland (BG); 1945, K. Sivertsen (BG). – Os, Söfteland, 1909, herb. F. Lange (O), nursery-garden, 1927, O. Hanssen (BG); Hegglandsdalen, 1927, O. Hanssen (BG); Hagavik, meadow at field, 1946, J. Naustdal (BG). – Jondal, Torvikbygd, Eidesvåg, garden, 1914, T. Lillefosse & S. K. Selland (BG). – Stord, garden, 1914, S. K. Selland (BG); Litlabö, adventitiously, 1920–1922, O. Hanssen (BG); Rommetveit, 1922, 1924, 1930, A. Röskeland (O). Some more coll. in Stord, latest 1930. – Ulvik, Hjeltnes, gardening school, 1918, S. K. Selland (BG) and 1951, N. Hauge (O). – Bruvik, Vaksdal (mill), 1918, J. Holmboe (BG) and H. Heiberg (BG); Dale, 1958, T. Ouren (BG). – Moster, Straumöy, garden, 1922, J. Holmboe (BG). Bömlo, Rubbestadneset, 1933, J. Gjerstad (TRH) and A. Röskeland (O). – Alversund, Fosse, roadside, 1923, T. Lillefosse (BG, O). – Kvinnherad, Husnes, Langåte, garden, 1924, T. Lillefosse (BG, O). Skånevik, Keimvik nursery garden, 1944, I. Jörstad (O). – Hosanger, Björsvik, 1927, O. Hanssen (BG). Fjell, Knarrevik, 1927, O. Hanssen (BG). – Asköy, Davangs mill, 1928, O. Hanssen (BG) – Varaldsöy, Haukås, garden, 1936, T. Lillefosse (BG). – Fana, St. Milde, garden, 1939, J. Naustdal (BG). Numerous adventitious coll. by J. Naustdal in Fana 1942–1960, a.o. in abandoned German camps. – Kvinnherad, Mauranger, weed, 1943, P. Störmer (O). – Modalen, Mo, Granheim, garden, 1953, I. Langedal (BG).

Sogn og Fjordane: Förde, at church, 1908, J. R. Landmark (BG). – Vik, garden, 1913, F. Jebe (O); Balvoll, garden, 1933, T. Lillefosse (BG). – Naustdal, Sunnfjord, Ytre Holmedal, field, 1896, O. Dahl (O); Sunnfjord, 1916, A. Landmark (O). – Aurland, Flåm, weed at Fretheim hotel, 1926, and 1929, R. Nordhagen (BG), Fretheim, 1933, O. Hanssen (O). – Hyllestad, Öen, Ulvik, garden wall, 1930, T. Lillefosse (BG, O). – Leikanger, parsonage, field, 1937, T. Lillefosse (BG, O). – Eid, Nordfjordeid, harbour, 1945, R. Nordhagen (BG). – Askvoll, Stongfjorden, 1951, J. Naustdal (BG). – Kinn, Brandsöy, nursery-garden, 1952, J. Naustdal (BG). – Vevring, Vevring farm, roadside, 1953, J. Naustdal (BG). – Jölster, Helgheim cemetery, 1959; Skude, nursery-garden, 1960, both O. Befring (BG).

Möre og Romsdal: Kristiansund, 1866, H. Greve (O). – Ålesund, near hospital, 1930, J. Lid (O); Aksla, 1938, R. Tambs Lyche (BG). – Norddal, Relling, 1932, O. Hanssen (O). – Volda, at road to Örsta, 1943, J. Kaasa (O). – Molde, Svenskebyen, 1947, S. J. Haukebö (O); Brendehaug nursery-garden, 1951, O. Röeggen (BG). – Sunndal, 1950, J. Haugen (TRH).

Sör-Tröndelag: Trondheim, Övre Allé, 1926, A. Lie (TRH); Kristiansten, 1938, O. A. Höeg

(TRH) and O. Andersen (TRH); Singsaker school, 1939, 1943, 1948, E. Fondal (GB, TRH), 1963, J 1068 (*10*). – Buvik, Pienes mill, 1935, E. Fondal (TRH).

Nord-Tröndelag: Namsos, Spillum garden, 1943, J. Roll-Hansen (TRH); grassy ground, 1950, K. Strompdal (TRH). – Stod, parsonage, path, 1950, J. Kielland Lund (O). – Egge, Vårtun, 1950, J. Kielland Lund (O).

Nordland: Vefsn, Halsöy, Nesbruket, weed, 1919; Ravnåmoane, at road, 1927. Mosjöen, Skjervengane, nursery-garden, 1944 (all three: P. Benum: Blyttia 8, p. 4, 1950). – Korgen, Leiraneset, nursery-garden, 1926, I. Jörstad (O). – Sömna, Berg, roadside, 1944 (Benum: op. cit.), garden wall, 1953, G. Strompdal (TRH).

Troms: Tromsö, garden, 1886, O. Nyhuus (O). – Lenvik, Finnsnes, roadside, 1934 (Benum: op. cit.). – Målselv, Andselv, nursery-garden, 1939, and 1948 (Benum: op. cit.). – Kvæfjord, Dale, roadside, 1944 (Benum: op. cit.). – Harstad, Ervika, nursery-garden, 1951. O. Finnseth (O).

Finland

Alandia: Without precise localities, C. E. Bergstrand: Bot. Not. 1852, p. 38. – Lemland, 1923, Franssila (H). – Mariehamn, 1951, 1954, A. Palmgren (H). – Kökar (O. Eklund: Die Gefässpflanzenflora beiderseits Skiftet, p. 218, 1958).

Regio aboënsis: Åbo, 1855, Wiklander (H); ballast (T. Sælan: Med. Soc. F. Fl. Fenn. 11, p. 213, 1885); harbour, 1886, N. Aschan (TUR). Several adventitious coll. up to present time. – Lojo, Maikala, field (Bot. Not. 1887, p. 38); Solhem, garden, 1901, H. Lindberg (H), 1912, H. Lindberg (Pl. Finl. exs. No. 672), 1916, V. A. Pesola (H). Jalassaari, Ahtiala, garden, 1942, H. Lindberg (Pl. Finl. exs. No. 1949). Some more coll. from Lojo. – Nagu, ditch at road, 1904, 1906, 1908, A. Dahl (H, UPS, TUR). – Maaria, Kärsämäki, lawn, 1925 (A. V. Auer: Mem. Soc. F. Fl. Fenn. 19, p. 67, 1944). – Karjalohja, park, 1946, Saarnijoki (H). – Iniö (O. Eklund: op. cit.). – Pargas, roadside, 1960, E. Mäkinen (TUR; is possibly a derivative of *R. austriaca* × *sylvestris* close to the latter). – Pojo, Fiskars, roadside, 1960, and refuse place, 1961, H. Sältin (H, TUR).

Nylandia: Borgå, Hammars, 1854, T. Sælan (H); ballast, 1856, Strömberg (H); Örnshamn, 1880, E. Öhrnberg (H, LD, S, TURA); near the sea, 1886, A. W. Gadolin (H, TURA); Ensalö, field, 1916, R. Boldt (H); in the town, 1949, Olavi (H). – Helsingfors, Sumparn, 1871, N. Sundman (H); 1871, T. Sælan (H); Observatoriebergen, refuse place, 1877, R. Hult (H). Numerous more adventitious coll. 1876–1963, e.g. J 1113 (*10*). – Esbo, Grankulla, road, 1903, G. Selin (H), 1915, R. Frey (H, TUR); park, 1949, Törnroth (H). – Kervo, railway, 1921, E. Häyrén (H), 1960, H. Roivainen (H). – Hangö, yard, 1942, L. Fagerström (H). – Sibbo, Myrans, at Kervo River, 1953, G. Marklund (H). Helsinge, 1961, J 439, J 441 (*10*). – Hyvinkää, cemetery, 1953, O. Pohjakallio (H). – Anjala, at L. Junkkarinjärvi, 1953, Mäkinen (H, TUR), U. Laine (TUR). – Lovisa, roadside, 1957, and ruderal place, 1961, F. Klingstedt (H). – Kyrkslätt, Obbnäs, at barracks, 1963, Å. Niemi (H).

Satakunta: Pori, Reposaari (= Räfsö), 1872, J. Sahlberg (H, TUR), 1879, H. Hjelt (H, TURA), 1901, Jakobsson (H), 1922, J. Gröntved No. 1241 (C), ballast, 1901, E. Häyrén (GB, H, UPS), "in saburra" 1901, T. Sælan (H), ditch, 1906, A. Lindfors (TUR). – Tyrvää, garden, 1915, V. Heikinheimo (Pl. Finl. exs. No. 1182). – Metsämaa, Kulankoski, at R. Konojoki, 1952, Salo (H). – [Eura, acc. to J. Jalas: Arch. Vanamo 8:2, p. 179, 1954, cf. App. 7.]

Tavastia australis: Jaala, Ilonoja, moist grassy ground, 1898, F. Klingstedt (GB, H). Iitti, grassy slope, 1899, W. Ramsay (H). – Urjala, Hangola, garden, 1950, L. Fagerström (H); Kivijärvi, Raikko, garden, 1950 and later, L. Fagerström (H), C. Brander (H), (L. Fagerström: Mem. Soc. F. F. Fenn. 29, p. 53, 1954). – Forssa, Kaukjärvi, gravelly ground, 1954, S. Toivonen (H); in the town, 1955, S. Toivonen (H). Tammela, church village,

roadside, 1958, L. Fagerström (H). – Hämeenlinna, 1957 (J. Tast: Luonnon Tutkija 63, p. 23, 1959). – Jämsä, Juokslahti, lake shore, 1959, A. Koskinen (H); Cf. A. Koskinen: Arch. Vanamo 18:4 p. 218, 1964. – Jämsänkoski, 4 localities (Koskinen: op. cit.).

Tavastia borealis: Jyväskylä, cemetery, 1949, E. J. Valovirta (H).

Savonia australis: Kouvola, railway station, 1932, A. Ulvinen (H), 1949 (V. Kujala & A. Ulvinen: Ann. Bot. Soc. Vanamo 35:2, p. 94, 1964). Kuusankoski, adventitiously, 1942, A. Ulvinen (H), 1943, O. K. Silkkilä (TUR). – Kangasniemi, church village, 1950, Suurinen (H).

Savonia borealis: Kuopio, street, 1909, K. Linkola (H). – Nilsiä, church village, 1915, O. Kyyhkynen (H). – Pielavesi, Taipale, adventitiously, 1925, O. Kyyhkynen (H).

Karelia australis: Kotka, 1882, K-lami (TURA); 1916, 1952. Kymi, cemetery, 1956 (all in Kujala & Ulvinen: op.cit.). – Trångsund (Uuras), 1901, Pacius (S). Viborg, Keikäsniemi, adventitiously, 1927, C. E. Sonck (H); Siikaniemi, adventitiously, 1934, V. Erkamo (H); Henttuala, 1934, V. Erkamo (H). – Hamina, harbour, 1952 (Kujala & Ulvinen: op.cit.; not in Fig. 13).

Karelia ladogensis: Sortavala, harbour, 1903, I. M. Wartiainen (H, TUR, TURA).

Karelia borealis: Lieksa, Pärnävaara, 1960 (C. E. Sonck: Acta Bot. Fenn. 67, p. 118, 1964).

Ostrobottnia australis: Vasa, Brändö (= Mustasaari), near church, 1892, Westerlind (H), 1895, Dahlberg (H, TURA), 1904, G. R. Idman (H), 1909, E. Nyström (H), roadside, 1893, Laurén (H). – Pörtom, church village, roadside, 1949, J. Montell (TURA). – Kaskö, harbour, 1945, Sundquist (H). – Kristinestad, harbour, 1945, E. J. Valovirta (H), 1946, A. Railonsala (H).

Ostrobottnia media: Jakobstad, Alholmen, ditch, 1896, C. W. Fontell (H, TURA).

Ostrobottnia kajanensis: Hyrynsalmi, Kangasjärvi, 1953, 1956, 1957, 1958, L. Heikkinen (H, LD). Cf. L. Fagerström: Mem. Soc. F. Fl. Fenn. 33, p. 53, 1958.

Ostrobottnia borealis: Oulu, harbour, 1902, Y. Wuorentaus (H).

Russian Fennoscandia (not mapped)

Karelia olonetsensis: Tokari, railway, 1943 (R. Repo: Arch. Vanamo 3, p. 74, 1949). Äänislinna (= Petrozavodsk), adventitiously, 1943, J. Jalas (H), R. Repo (H), Pankakoski & Äyräpää (H). Jyrkilä, Vieljärvi, meadow and at brook (L. Fagerström & H. Luther: Mem. Soc. F. Fl. Fenn. 21, p. 25, 1946).

Karelia pomorica occidentalis: Mouth of the Kem River, A. O. Kihlman (Fagerström & Luther: op. cit.).

Iceland (not mapped)

Borgarfjarðarsýsla: Reykholt, garden, 1936, S. O. F. Omang (ICEL).

Eyjafjarðarsýsla: Árskógur, 1953, I. Davíðsson (C).

Árnessýsla: Biskupstungur, Birkislund, with Norwegian tree plants (I. Davíðsson: Náttúrufræðingurinn 29, p. 39, 1959).

Gullbringusýsla: Reykjavík, airport, 1959 (I. Davíðsson: Náttúrufræðingurinn 30, p. 41, 1960).

Appendix 5. Scandinavian collections of *Rorippa amphibia* × *sylvestris*

Unverified literature reports have not been considered. Skåne collections from the same water system and Mälar collections covered by one symbol in Fig. 16 are grouped together within dashes. For further explanations see p. 167.

DENMARK

Jylland: D 27. Ribe, 1851, D'ORIGNY (C, cf. App. 4), 1883, O. GELERT (C, LD), 1885, herb. LANGE (C), 1906, M. ENGSTEDT (S); S. of the town, meadow, 1919, S. ANDERSEN (C); at Ribershus, 1947, H. P. KRISTENSEN (C). D 6. Thy, Hvide R., 1866, J. P. JACOBSEN (C). *Sjælland:* D 41. Korsör, Tjæreby, Veisgård, 1870, P. NIELSEN (C). *Bornholm:* D 47. Nexö, 1928, C. O. PLENGE (C); fen N. of the town, 1937, 1938, S. ANDERSEN (C).

SWEDEN

Skåne: Lund, Källby, stream [= R. Höje å], 1834 and 1873, Anon. (LD), 1885, E. BJÖRLING (GB, LD), 1918, 1920, O. HOLMBERG (GB, LD, O). "Lund", 1882, BJÖRLING (GB, LD). Flackarp, Trolleberg [at R. Höje å], 1885, S. MURBECK (LD) and C. LÖWEGREN (LD), 1917, C. BLOM (GB). At R. Höje å, 1920, T. BRANDT (GB, LD, S, TURA). Lomma, 1885, SKOTTE (LD); 1891, N. JOHNSON (LD); riverside [R. Höje å] near the church, and meadow between Alnarp and Arlöv, both 1934, G. NORRMAN (LD). – Burlöv, Arlöv, 1885, C. PAULSSON (LD), 1894, G. JOHANSSON (GB, LD, O) and A. ANDERSSON (LD), 1897, C. MAGNUSSON (LD) and W. BORGQUIST (BG, GB, H). – Löddeköpinge [?], Löddeström, 1881, S. MURBECK (LD). Örtofta, Mellanmöllan, 1881, S. MURBECK (BG, LD). V. Hoby, Krutmöllan, 1886, G. A. KARLSSON (GB, LD, S), 1888, 1908, 1909, 1913, E., H. or K. VALLIN (GB, LD, O, S, TURA, UPS). Lackalänga, at the river [= R. Kävlingeån], 1868, H. M. RAMBERG (BG); 1895, ODHNER (H); 1961, J 532. Örtofta, 1883, G. ANDERSSON (S); 1925, T. LANGE (TURA). Hög, Höjsmöllan, 1893, J. WIDE (GB). Håstad, Kvarnvik, 1925, H. NILSSON (LD); 1925, C. BLOM (GB). – At R. Sege å, 1884, T. SJÖVALL (GB), 1886, F. BLOCK (H), 1887, A. PIHL & F. BLOCK (GB, H, LD, S). Börringe, at R. Sege å, 1907, S. SELANDER (S). N. Skrävlinge, 1931, N. JOHNSON (LD, S); 1961, J 534. – S. Åsum, 1886, A. & A. ROTH (GB, H, LD, UPS) and H. THEDENIUS (S); 1887, A. BERG (S); 1961, J 543. Tolånga, 1898, F. ENGFELDT (BG, LD, S), 1905, 1906, S. & H. THUVESEN (BG, GB, H, LD, O, S, TURA, UPS, UPSV), 1906, K. MATTSSON (H, UPS), 1907, O. HASSLOW (GB, H, LD, S, TURA), 1908, G. JÖNSSON (BG, GB, LD, TURA). – Raus, Råå, 1895, S. RAAB (UPS). – Nosaby, 1898, O. HOLMBERG (LD). Kristianstad, 1908, at a canal, 1929, 1932, 1933, meadow, 1935, P. TUFVESSON (H, LD); 1909, G. TURESSON (GB, TURA); 1917, O. HASSLOW (BG, GB, TURA); 1922, T. LANGE (GB, TURA); 1963, J 1085. Åhus, at R. Helge å, 1913, 1914, F. H. ANDER (LD, UPS); Yngsjö, 1924, P. TUFVESSON (LD). Gärds Köpinge, 1929, P. TUFVESSON (LD, O), 1930, L. LINDQVIST (GB). N. Åsum, Lillö, 1936, 1939, P. TUFVESSON (C, H, LD). – Vomb, at R. Kävlingeån, and at dry branch of the river, 1946, J. LINDERS (LD). At L. Vombsjön, Vomb, 1946, 1947, J. LINDERS (LD) and 1961, J 536; Harlösa, 1963, J 1095; Öved, 1963–65, J 1091, J 1236–1237, J 1311. – Husie, 1961, J 535. – Fränninge, 1965, J 1312, J 1314. *Östergötland:* Vreta Kloster, 1888, N. REDELIUS (S). *Närke:* Örebro, Ekebäck, 1898, G. BÅGENHOLM (LD). *Södermanland:* Torshälla, Väsby, 1839, herb. HARTMAN (UPS); Väsbyviken, 1864, herb. SÖDERBERG (TURA). – Strängnäs, 1888, 1889, W. WERNSTEDT (BG, H, LD, S), 1888, H. FORSSMAN (LD, S); Visholmen, 1888, E. KÖHLER (BG, H, O, TURA, UPS); Nabbviken, 1916, A. WOLLERT (LD, S, UPS); 1964, J 1222 (*17*). – Sundby, Sundbyholm, 1903, RIDDERSTOLPE (S),

1961–1964, J 339 (*17*), J 920 (*17*), J 1260. – Barva, at L. Mälaren, 1906, C. & S. Cederblad (UPS). *Uppland:* Uppsala, Kungsängen, 1818, G. Wahlenberg (UPS), 1854, 1863, K. J. Lönnroth (O, UPS, UPSV) 1855, 1857, E. P. Fries (UPS, UPSV), 1861, T. O. B. N. Krok (S), P. Olsson (UPS, UPSV) and U. Walmstedt (LD, S), 1891, C. M. Broström (UPS); at R. Fyrisån [= Kungsängen], herb. E. Fries (UPS), J. E. Wikström (S), 1821, Indebetou (S), 1837–41, F. Graewe (S), 1844, N. J. Andersson (S), 1854, R. Fristedt (S), 1857, Zetterstedt (UPS) and T. O. B. N. Krok (S), 1873, P. Rosén (S), 1892, G. A. Fröman (H, UPSV); Islandet, 1850, Th. M. Fries (UPS); L. Föret, 1861, W. E. Berndes (LD); without prec. loc., prob. Kungsängen, "af Wg", herb. Hartman (UPS), E. Fries (Herb. norm. Nos. VI. 18 and XI. 36), Bjurzon (S), 1835, P. A. Sohlman (S), 1847, C. Hartman jr (UPS), 1855, E. P. Fries (UPSV), 1889, E. Holmgren (UPS). Bondkyrka, Ultuna, 1873, P. Borén (BG, H, LD, TURA, UPS, UPSV), 1871, 1881, N. F. Ahlberg (UPS, UPSV), 1884, J. A. O. Skårman (LD, S, TURA), 1889, H. Fries (UPS); Flottsund, 1854, E. P. Fries (UPS, UPSV); between Flottsund and Vårdsätra, 1858, C. P. Laestadius (H); Vårdsätra, 1871, H. Lundberg (H, S, UPS, UPSV); Vårdsätra kvarn (Lurbo) at R. Hågaån, 1939, E. Almquist (UPSV), 1960, N. Lundqvist No. 2467 (UPS), 1961, J 385 (*17*), J 387 (*17*), J 394, = Uppsala-Näs, Lurbo, 1921, E. Almquist (UPSV). – Dalby, Säbyklint, Wahlenberg (K); Hammarskog, 1886, O. F. Andersson (S); Dalbyudd, 1944, E. Almquist (UPSV), 1962, J 924 (*17*); 1962, J 1224 (*17*). – Uppsala-Näs, Vreta, 1886, O. F. Andersson (S). – Ed, Stäket, 1844, N. Lagerheim (UPS), 1917, V. Laurent (S); – Runsa, 1933, E. Almquist (UPS). – Sigtuna, 1858, herb. Cederstråhle (S); 1881 and Viby, 1889, M. Floderus (H, LD); 1903, O. Sjöberg (S); 1961–1964, J 526, J 1253. S:t Olov, Lövstaholm, at L. Garnsviken, 1882, A. L. Segerström (S). S:t Per, 1887, O. F. Andersson (LD). – Alsike, Flässjan, 1860, J. Henschen (UPS); Krusenberg, 1866, H. Holmberg (S), 1897, H. Jahnke (UPSV). – Häggeby, herb. Hartman (UPS); 1962, J 936 (*17*). – Övergran, 1961, J 355 (*17*). – Yttergran, 1961, J 356 (*17*). – Enköping, 1879, T. Floderus (S). Svinnegarn, 1961, J 371 (*17*), 372. – Skokloster, 1882, J. A. O. Skårman (LD, UPS, UPSV); 1887, O. F. Andersson (H, S, TURA); Väderkvarnsbacken, at L. Mälaren, 1915, G. Björkman (UPSV); Kronudden, 1925, G. Björkman (H, UPSV); Arnöhuvud, 1953, E. Almquist (S), 1962–1964, J 933–935 (*17*), J 1244–1251 (*17*); 1961, J 344 (*17*), 347 (*17*); 1966, J 1541, 1542. – Vassunda, Ekhamn, 1910, G. Cedergren (UPSV). Haga, Torsborg, 1924, K. Björkman (UPS). – [Probably this hybrid: Svartsjö, 1885, H. Fröding (UPS). Järfälla, Kallhäll, 1917, V. Laurent (S). Lovö, Drottningholm, 1919, T. Vestergren (S).] *Västmanland:* Västerås, harbour, 1884, A. E. Luhr (S). Rytterne, Nyckelön, 1913, 1919, G. Lindmark (S, TURA, UPS), 1962, J 921 (*17*), 1262. [*Hälsingland:* possibly this hybrid: Hudiksvall, Bränslet, 1913, A. Nordström (GB, UPS).]

[Norway

Possibly this hybrid: *Hordaland:* Odda, at factories, 1911, S. K. Selland (O).]

Finland

Ostrobottnia borealis: Alatornio, Keropudas, 1959, E. Asplund (S), and E. Julin (UPS), 1961, J 520.

Appendix 6. Scandinavian collections of *Rorippa austriaca*

For explanations see p. 167.

DENMARK

Jylland: D. 13b. Randers, 1914 and 1923, H. JENSEN (C). D. 25. Vejle, harbour, 1916 and 1928, S. ANDERSEN (C). D. 6. Thisted at Dragsbæk, near brewery, 1917, C. H. OSTENFELD (C); 1934, N. GRÖNKJÆR (C). D. 1. Kvissel at the brickyard, roadside, 1921, S. ANDERSEN (C); 1946, H. S. DAHL (C) and LINDHARD (AAU). Skagen, Locher's Ville, on sand-dunes, 1932, C. CHRISTENSEN (C); waste place, 1966, A. HANSEN (C). D. 26. Tistrup, poultry farm, 1931, (?) (C). D. 51. Lögumkloster, 1951, A. VESTERDAL (C). D. 17. Nörre Nebel, at railway, 1951, K. LARSEN (C), 1964, A. HANSEN (C) and 1966, J 1552. D. 27. Kvong, ditch near dairy, 1957, A. HANSEN (C). *Fyn:* D.29. Odense, Tolderlund, waste place, 1935, 1951, H. EILSTRUP (C); harbour, 1962, M. RASMUSSEN (C). *Sjælland:* D. 46. Köbenhavn, Lersöen, waste place, 1919, E. SCHÄFFER (C). D. 42. Kaldred, roadside, 1942, S. ANDERSEN (C). D. 39a. Lundby, 1950, PONTOPPIDAN (C).

SWEDEN

Skåne: Hälsingborg, field, 1941, T. LANGE (S, UPS), waste place, 1951, E. ASPLUND (S). Barkåkra, Vejbystrand near the beach, 1958, I. GUSTAVSSON (LD); Varehög, 1958, S. KILANDER (UPS). *Småland* (Klm): Kalmar, on slime, 1908 and Malmbron, 1909, S. MEDELIUS (O, S, UPS); ballast, 1911, F. R. AULIN (S). *Västergötland* (exc. Gbg): Mariestad, mill at R. Tidan, 1915, B. NILSSON (S); at R. Tidan opposite Mariesjö, 1917, A. HÜLPHERS (GB, S, UPS). *Göteborg region* (Gbg): Synneröd, farm, 1945, H. FRIES (GB, S, UPS). *Södermanland:* Stockholm, Brännkyrka, Gamla Årsta Äng, 1924, J. LAGERKRANZ (S).

NORWAY

Östfold: Moss, waste place by R. Mosselven, 1927, J. HOLMBOE & J. LID (BG, O, S); Skåtöy, Örvik, 1931 (R. TAMBS LYCHE: K. Norske Vidensk. selsk. Skr. 1934, 5, p. 9); at factory, 1956, J. SULENG (O); garden weed, 1962, T. JÖRGENSEN (O). Onsöy, Engelsköya, 1956, A. EFTESTÖL (O; publ. as *R. amphibia* in Blyttia 18, p. 89, 1960). *Akershus:* Oslo, Grönlien, Ekeberg, 1909, R. FRIDTZ (O); Thorehaugslökken, introduced with cereals, 1915, H. JOHNSEN (O) and Thorehaug, 1915, 1917, A LANDMARK (O), 1916, E. TRÆTTEBERG (O); Grefsen, weed in garden, 1930 and 1932, A. RÖSTAD (O), 1933, K. KLAVENESS (O). *Buskerud:* Drammen, mill, 1932, O. HANSSEN (O). Hurum, at Tofte factories, 1945, P. STÖRMER (O). *Telemark:* Skien (Gjerpen), at silo, 1908 and 1909, H. JOHNSEN (O, S), 1909, J. DYRING (BG), 1911 and 1912, A. LANDMARK (O). Kviteseid, Midsund, pasture, Voll, pasture and Brunkeberg, all 1957, J. LID (O). Porsgrunn, old quay at the river, 1964, T. OUREN No. 24964 (O). *Vest-Agder:* Oddernes, Mosbö, at the stream Höiebekken, 1908, A. RÖSKELAND (O). Randesund, Torsvik, 1909, T. RUUD (O), and H. BENESTAD (O). Kristiansand, Lund, 1935, J. NULAND (O). *Rogaland*: Strand, Tau, 1952, H. B. GJÆRUM (O); Tau mill, 1953, M. BÖDTKER (BG). Madla, Madlalia, 1963, I. LIMA (BG). *Hordaland:* Bergen, Hæggernes mill, 1911, 1918, 1920 and 1923, J. HOLMBOE (BG, O), 1925, S. SLETTEMARK (BG), 1929, K. FÆGRI (BG), 1930, M. BÖDTKER (O), 1939, R. NORDHAGEN (BG), 1942, G. KNABEN (BG), 1958, 1961, 1962, 1963 and 1964, T. OUREN a.o. Nos: 21509, 23687, 23950, 25012 (BG). Bruvik, Vaksdal (mill), 1915, J. LID (BG, O), 1918 and 1920, J. HOLMBOE (BG), 1918, H. HEIBERG (BG), 1928, O. HANSSEN (BG); Bruvik (mill), 1928, O. HANSSEN (BG). Jondal, Torvikbygd, Eidevåg, 1914, S. K.

Selland (BG, O) and poultry yard, 1914, T. Lillefosse (BG), roadside, 1927, V. Rosseland (O); Asköy, Olavik, with planted larch trees, 1917, T. Lillefosse (BG, O). Fitjar, Stord, Vestbostad, poultry yard, 1919, J. Lid (BG). Holsnöy, Meland, at schoolhouse, 1954, G. Aarhus (BG). Laksevåg, Oldernes, 1956, M. Bödtker (BG). *Sör-Tröndelag:* Strinda, near Kroppa mill, 1908, N. Hvoslef (O); Selsbakk, by R. Nidelven, 1918, R. Tambs Lyche (O). Buvik, Pienes mill, 1924, R. Tambs Lyche (O).

Finland

Tavastia australis: Kuusankoski, Kymmene Bruk, roadside near railway, 1950, F. Klingstedt (H). *Isthmus karelicus:* Terijoki, Kellomäki, railway station, 1933, Jäppinen (H), 1935, L. Fagerström (BG, H, S, UPS); Keskikylä, railway, 1935, L. Fagerström (H).

Appendix 7. Scandinavian collections of *Rorippa austriaca* × *sylvestris*

Unverified literature reports have not been considered. For explanations see p. 167.

Denmark

Jylland: D. 52. Store Okseö in Flensburg F., 1923, C. H. Ostenfeld (C)[1] and 1965, A. Hansen (C). D. 10. Hvalpsund, 1939, K. Wiinstedt (C) and Lindhard (AAU). D. 13b. Gjessinggård near Randers, 1940, K. Wiinstedt (C). D. 22b. Djursland, N.E. of Gjerrild, roadside, 1961, A. Hansen (C); N. of Grenå at the road Troldhöj–Gjerrild, 1965, E. Wersöe (C). D. 10/13 b. Sjörring, by tributary to R. Skalsåen, 1965, E. Wersöe (C). D 25. Hejls S.E. of Kolding, 1962, J 872. D. 11. Hobro, Rörbæk, weed, without date, P. M. Pedersen (C)[1]. [Probably this hybrid: *Fyn*: D. 32. Drejö, grassy ground, 1947, L. Kring (C)[1].] *Sjælland:* D 46. København near Bispebjerg hospital, 1927, S. Andersen (C)[1]. Vangede, Gammelmosevej, 1961, and Amager, 1963, J. Eliasen (C). D. 45 b. Hornbæk, railway station, 1933, C. Blom (C, GB, LD, UPS); 1944, A. Vesterdal (C). Hilleröd, at the road to Lilleröd, 1943, J. Mikkelsen (C); roadside S. of town, 1951, K. Larsen (C). Birkeröd, Lollikhus, and Rudersdal, 1944, 1945, 1950, S. Andersen (C, LD, UPS). Frederiksværk, 1962, J 868. D. 45a. Buddinge railway station, 1942, H. S. Dahl (C). Gentofte, garden, 1943, H. S. Dahl (C)[1]. Holte, 1944, H. S. Dahl (C) and Lindhard (AAU). Herlev railway station, 1961 and 1964, A. Hansen (C). D. 44. Hornsherred, Brandbjerg, 1946, K. Wiinstedt (C)[1]. D. 39 b. Faxe, Hovby, 1962, N. Jensen (C). [Probably this hybrid: Hornsherred, Venslev Strand, 1917 and 1918, K. Wiinstedt (C)[1].]

Sweden

Skåne: Malmö, at the turbine, 1909, A. Kemner (LD, UPS) and 1916, C. Blom (GB, UPSV); harbour, 1913, Johansson (LD, TURA); Limhamnsfältet, 1913 and 1915, J. G. Gunnarsson (GB, LD, S); near Kockum's, dry sandy ground, 1927, G. Norrman (LD): [Probably also: 1907, D. Hylmö (LD)]. Kristianstad, Långebro, 1928 and later, P. Tufvesson (C, GB, H, LD, O). Eljaröd, Tjörneröds mölla, field, 1947, M. Nilsson (GB, LD), 1963, J 1090. Stoby, 1961, J 540. Gumlösa, 1961, J 541. Osby, 500 m NNW of the church, 1961, S. Snogerup (LD). *Blekinge:* Sölvesborg, 1932, G. Björnström (LD). [*Småland* (probably this hybrid): Växjö, 1915, 1934 and 1935, A. S. Trolander (GB, O, S); W. shore of L. Växjösjön, 1915 and 1919,

[1] In Pedersen (1958) as probably *R. amphibia* × *sylvestris*.

C. Pleijel (S).] *Gotland:* Endre, Hulta, poultry farm, 1939, E. T. Fries (GB, LD, S, UPS). *Västergötland* (exc. Gbg): Lerum, N. of Slätthult, 1930, K. F. Lindgren (GB); [probably also Aspenäs, 1927, F. Lundberg. Borås, Östra Enedal, 1934, 1936, C. Sandberg (LD, O, GB, S, UPS, TUR; in e.g. Hasselrot (1967) as *R. amphibia* × *sylvestris*); at road to Ulricehamn, 1934 and 1937, G. A. Westfeldt (UPS); at a new hospital, 1937, G. A. Westfeldt (UPS); Björkängsvallen, 1953, Ö. Nilsson (LD); Rya, roadside, and Hultasjön, roadside, 1966, G. A. Westfeldt (UPS); Gingri, Tosseryd at a farm, 1937, C. Sandberg (GB, LD, UPS). St. Lundby, Björboholm, shore of L. Mjörn, 1939; J. A. O. Skårman (GB, UPS). Brämhult, St. Borhult, 1966, G. A. Westfeldt (UPS). *Halland:* Sibbarp, between Stegared and Åkulla, ditch by the road, 1931, C. Blom (Samuelsson: Pl. Suec. exs. No. 903). Knäred, church village, dry field margin, 1940, C. Blom (GB, LD, S, UPS); roadside between railway station and highway, 1952, F. Lundberg (GB). *Göteborg region* (Gbg): Göteborg, V. Frölunda, Sandarne, 1918 and 1920, E. Hjertman (GB, LD, O, UPS), 1931, B. Nilsson & G. Degelius (UPS); Högsbotorpen, 1924, H. Fries (GB), 1930, C. Blom (BG, GB, O, UPS), 1931, K. Anderberg (GB) and L. Lindquist (GB); Katrinedal (Levgren's meadow), 1923, R. Ohlsén (GB), 1927, B. Nilsson (UPS), 1933 and 1934, E. Hjertman (GB), 1934, C. Blom (GB), 1955, H. Fries (GB); Olskroken, 1930, H. Fries (S) and R. Ohlsén (GB, UPS); Änggården, 1947, C. Blom (GB, H); near Ekebäck, waste place, 1957, C. Blom (GB, LD, S). Mölndal, Fässberg, 1941, C. Hjärne (GB). *Bohuslän:* Ljung, Lyckorna, 1920, C. G. H. Thedenius (GB, TUR) and G. Degelius (UPS); Ljungsgård, 1931, H. Fries (GB, LD, S); between Ljungskile and Tjöstelsröd, roadside, 1952, H. Fries (GB); at innermost part of Ljungskile Bay, 1966, M. Ohlander (GB). Uddevalla, S. Harbour, 1953, H. Fries (GB). *Uppland:* Stockholm, Djurgården, Friesen's Park and Biskopsudden, 1919, Haegerstolpe (S) and T. Vestergren (S); 1925, C. A. Falkenberg (S); Oakhill, roadside, 1928, J. R. Jungner (S). Skeppsholmen, lawn, 1937, N. Hylander (GB, S, UPS). Vittinge, Friberg, field margin, 1950, E. Almquist (S, UPS). *Dalarne:* Rättvik, railway station, 1922, O. Juel (UPS) and G. Samuelsson (LD, UPS). Avesta, 1925, K. F. Hollström (S). Borlänge, Domnarvet ironworks, 1933, 1935 and 1943, J. B. Bengtsson (GB, LD, S, UPS, TUR). Grängesberg, N. of railway station, 1934, E. Almquist (S). Ål, Ekhagen, clover pasture, 1942, I. Ambjörn (S). *Hälsingland:* Ljusdal, Hovsberg, roadside, 1934, G. Lidman (Samuelsson: Pl. Suec. exs. No. 904) and 1935, G. Lidman (O). *Medelpad:* Njurunda, shore of L. Döviksjön, 1951, E. Höij (collector's herb.). *Ångermanland:* Örnsköldsvik, roadside, 1939, G. R. Cedergren (S).

Norway

Östfold: Moss, C. S. Størmer (O); at ship-yard, 1949, J. Suleng (O); Jælöy, Værla, 1947, O. Röseng (O, UPS). Halden, Nedre Remmen, 1946, H. Suleng (O). *Akershus:* Oslo, Sagene 1905, R. E. Fridtz No. 12567 (O); Bygdö, Bygdönes, 1910, H. Johnsen (LD, O), 1912, J. Lid (O), 1913, C. Leegaard (O), 1914, E. Trætteberg (O); park at the Royal Castle, 1916, J. Dyring (BG, O), 1964, J 1220; Grefsen, garden, 1930 and 1932, A. Röstad (O), 1933, Klaveness (O); Grefsen, near Bakke mill, 1941, F. C. Sörlye (O); Vækerö, field, 1938, P. Størmer (O); Aker, Storo, 1941, P. Størmer (O), 1941 and 1951, J. Lid (C, O; publ. as *R. amphibia* in Blyttia 18, p. 89, 1960); Tuengen Allé, 1961, P. Størmer (O); T. Segerstedts Vei, 1962, J 856; [probably this hybrid: Eilert Lunds Gate, 1911, A. Landmark (O)]. Nittedal, Glittre Sanatorium, 1937, and Hakadal, 1939, A. Vilke (LD). Rælingen, Lilleström, at railway bridge, 1944, J. Lid (O), 1954, P. Størmer (O). Bærum, road below Kolsås railway station, 1942 and 1943, F. Lange (O). *Oppland:* Fluberg, Odnes, 1909, R. Fridtz (O). Gjövik, mouth of R. Hunnselven, 1936, J. Holmboe (O). *Buskerud:* Drammen, Aktienvei, 1932, O. Hanssen (O). Modum, Åmot, agricultural school, 1942, J. B. Heldal (O). Sigdal, Eggedal, Hamre, 1943, K. Tylden (O). Hurum, Tofte factories, 1945, P. Størmer (O). Lier, Reistad, 1946 and

Hegg, roadside, 1946, P. Störmer (O). *Vestfold:* Tönsberg, Slottsfjellet, 1960, S. Kaasa (O). *Telemark:* Sannidal at Kråkerö, Rinde, 1940, J. Lid (O), Seljord, Valler Bru, 1958, J. Lid (O) and 1960, K. Andreassen (O). Gjerpen, Kulten, roadside, 1958 and Borgestad, field margin, 1963, O. Svendsen (O). Bö, Nedre Grivi, 1959, J. Lid (O). Tinn, Öystebygdi church, 1959, K. Andreassen (O). *Vest-Agder:* Sögne, Klappland, at the school, 1947, P. Störmer (O), 1959 and 1960, A. Björndal (O); near the dairy, 1960, A. Björndal (O). *Hordaland:* Kvam, Ålvik, garden, 1954 and 1955, K. Sivertzen (BG, O, S).

Finland

Regio aboënsis: Åbo, Hirvensalo, ditch at road, 1954, Ahtola (H); 1959, E. Mäkinen (TUR). *Nylandia:* Hangö, meadow, 1932, E. Niemi (H) and Haapala (H), 1953, P. Isoviita (H). Helsinge, Sentula, 1950, V. Erkamo (H). Sibbo, Hitå, 1954, G. Marklund (H); *Satakunta:* Eura, Kauttua, at river-shore opposite factory, 1945, F. W. Klingstedt (H, publ. as *R. sylvestris* in J. Jalas: Arch. Vanamo 8:2, p. 179, 1954); 1962, I. Kause (TUR). *Tavastia australis:* Jämsänkoski, Virtasalmi, 1959, A. Koskinen (H; publ. as *R. amphibia* × *sylvestris* in Arch. Vanamo 18:4, p. 218, 1964). *Savonia australis:* Ruokolahti, Immola, field, 1921, K. Linkola (H). *Karelia australis:* Vuoksenranta, Sintola, field, 1922, A. Pulli (H). Antrea, Ikävalkola, railway, 1923, O. H. Porkka (H); 1936, V. Erkamo (H). *Karelia ladogensis:* Sortavala, park, 1922, K. H. Hällström (H). *Isthmus karelicus:* Terijoki, Kellomäki, railway, 1933, Jäppinen (H); 1937, V. Erkamo (H).

REFERENCES

Abrams, L. 1944. *Illustrated Flora of the Pacific States II.* Stanford.

Ahlfvengren, F. E. 1924. *Hallands växter.* Lund.

Ahti, T. 1962. On the taxonomy of Erysimum cheiranthoides L. (Cruciferae). *Arch. Soc. Vanamo 16*, pp. 22–34.

Allioni, C. 1785. *Flora Pedemontana I.* Augustae Taurinorum.

Alm, C. G. 1944. Om Carex macloviana d'Urv. och dess utbredning i Nordeuropa. *The Svedberg 1884 30/8 1944*, pp. 578–600. Uppsala.

Almquist, E. 1929. Upplands vegetation och flora. *Acta Phytogeogr. Suec. 1.* Uppsala.

—— 1948. Utbredningstyper i upplandsfloran. *Natur i Uppland*, pp. 48–66. Göteborg.

—— 1949. *Dalarnes flora.* Lund.

—— 1957. Järnvägsfloristiska notiser. Ett apropos till järnvägsjubileet. *Sv. Bot. Tidskr. 51*, pp. 223–263.

—— 1965. *Flora upsaliensis. Uppsalatraktens växter.* Uppsala.

Alston, A. H. G. 1957. A Linnaean Herbarium in Paris. *Proc. Linn. Soc. London 168*, pp. 102–103.

Ambrosiani, B. 1961. Långhundraleden. *Uppland 1961*, pp. 7–33. Uppsala.

Anderson, E. 1949. *Introgressive Hybridization.* New York and London.

Arell, F. 1915. *Svenska statsbanornas stationer*, ed. 2. Uppsala.

Areschoug, F. W. C. 1881. *Skånes flora*, ed. 2. Lund.

Babcock, E. B. 1947. The Genus Crepis. 1. *Univ. Calif. Publ. Bot. 21.* Berkeley and Los Angeles.

Ball, P. W. 1961. The identity of Sisymbrium pyrenaicum L. ex Loefl. and later homonyms. *Feddes Repertorium 63*, pp. 14–17. Berlin-Dahlem.

Bauhinus, C. 1620. *Prodromos Theatri botanici.* Francof. a. M.

—— 1623. *Pinax theatri botanici.* Basiliae.

Baumann, E. 1911. *Die Vegetation des Untersees* (Bodensee). Stuttgart.

Beal, E. O. & Monson, P. H. 1954. Marsh and aquatic angiosperms of Iowa. *Univ. Iowa Stud. Nat. Hist. 19*, pp. 1–95.

Becherer, A. 1930. Fortschritte der Floristik. Gefässpflanzen. *Ber. Schweiz. bot. Ges. 39*, pp. 79–101.

Beck von Managetta, G. R. 1890–93. *Flora von Nieder-Österreich.* Wien.

Bennett, A. 1909. Nasturtium palustre DC. in Orkney. *Ann. Scott. Nat. Hist. 1909*, pp. 53–54.

Benum, P. 1958. The Flora of Troms Fylke. *Tromsö Museums skr. 6.* Tromsö.

Bergeret, J. P. 1784. *Phytonomatotechnie universelle III* (*Crucifères françaises*). Paris.

Berggren, G. 1962. Reviews on the Taxonomy of Some Species of the Genus Brassica, Based on Their Seeds. *Sv. Bot. Tidskr. 56*, pp. 65–135.

Bergstedt, N. H. 1883. Bornholms Flora. *Bot. Tidsskr.* 13, pp. 133–198.

Besser, V. S. 1822. *Enumeratio plantarum hucusque in Volhyniae, Podoliae.*, Vilnae.

Błaszczyk, H. 1953. Nowe stanowiska Rorippa austriaca (Crantz) Bess. i uwagi o Rorippa cracoviensis Zap. *Fragmenta florist. geobot. 1*, pp. 96–100. Kraków.

Blom, C. 1931. En för Sveriges flora ny hybrid, Roripa austriaca (Crantz) Bess. × silvestris (L.) Bess. *Medd. Göteborgs bot. trädg. 6*, pp. 145–150.

Böcher, T. W. 1938. Biological Distributional Types in the Flora of Greenland. *Medd. om Grönland 106:2*. Köbenhavn.

Böcher, T. W., Holmen, K. & Jakobsen, K. 1966. *Grönlands flora*, ed. 2. Köbenhavn.

Boissier, E. 1867. *Flora orientalis I.* Genevae.

—— 1888. *Flora orientalis. Supplementum.* Genève.

Borbás, V. 1878. Vizsgálatok a hazai Arabisek és égyeb Cruciferák körül. *Mathem. természettudom. közlemények 15*, pp. 145–212. Budapest.

—— 1879*a*. Floristicai adatok különös tekintettel a Roripákra. *Értek. természettudom. köréből 9:15*. Budapest.

—— 1879*b*. Eine ungarische Crucifere mit vierfächeriger Frucht. *Österr. bot. Zeitschr. 29*, pp. 246–247.

—— 1882. Roripa anceps und R. Sonderi. *Ibid. 32*, pp. 42–44.

Borsos, O. 1951. A mesterséges életfeltételek alakitó hatása a Rorippa- és Achilleafajokra. *Ann. biol. Univ. Hung. 1*, pp. 173–195. Budapest.

—— 1967. Über einige Rorippa- und Veronica-Arten. *Acta bot. Acad. scient. Hung.* 13, pp. 1–10.

Brandt, J.-P. 1961. Cytotaxinomie et cytogéographie de Veronica prostrata L. *Bull. Soc. neuchât. Sci. nat. 84*, pp. 35–88.

Braun-Blanquet, J. 1923. Über die Genesis der Alpenflora. *Verh. Naturf. Ges. Basel 35*, pp. 243–261.

Britton, C. E. 1909. A Radicula Hybrid. *Journ. of Bot. 47*, p. 430.

— - 1920. Report for 1919. *Rep. Bot. Soc. Exch. Club Brit. Isles 5*, p. 806.

Bronckers, F. 1963. Variations polliniques dans une série d'autopolyploides artificiels d'Arabidopsis thaliana (L.) Heynh. *Pollen et spores 5*, pp. 233–238.

Brügger, C. 1860. Zur Flora Tirols. *Zeitschr. Ferdinand. Tirol u. Vorarlberg 3. Folge, 9:5*. Innsbruck.

Busch, N. 1913–31. *Flora Sibiriae et Orientis extremi*. Leningrad.

Butters, F. K. & Abbe, E. C. 1940. The American varieties of Rorippa islandica. *Rhodora 42*, pp. 25–32.

Cajander, A. K. 1905. Beiträge zur Kenntnis der Vegetation der Alluvionen des nördlichen Eurasiens II. Die Alluvionen des Onega-Thales. *Acta Soc. Sci. Fenn. 33:6*. Helsingfors.

—— 1909. Beiträge zur Kenntnis der Vegetation der Alluvionen des nördlichen Eurasiens III. Die Alluvionen der Tornio- und Kemi-Thäler. *Ibid. 37:5*. Helsingfors.

Čelakovský, L. 1874. *Prodromus der Flora von Böhmen III.* Prag.

Černohorský, Z. 1947. Graines des crucifères de Bohême. *Opera bot. čech. 5*. Prague.

Christiansen, W. 1953. *Neue kritische Flora von Schleswig-Holstein*. Rendsburg.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. 1962. *Flora of the British Isles*, ed. 2. Cambridge.

Clausen, R. T. 1941. On the use of the terms "subspecies" and "variety". *Rhodora 43*, pp. 157–167.

Crantz, H. J. N. 1762. *Stirpium austriarum fasciculus I.* Viennae Austriae.

Dahl, O. 1912. Botaniske undersökelser i Helgeland I. *Videnskapsselsk. Skr. I. Mat.-nat. Kl. 1911, 6*. Kristiania.

—— 1934. Floraen i Finnmark Fylke. *Nyt Mag. Naturvidensk. 69*. Oslo.

Dalla Torre, K. W. v. & Sarnthein, L. v. 1909. *Flora von Tirol, Vorarlberg und Liechtenstein II*. Innsbruck.

Dandy J. E. 1958. *List of British Vascular Plants*. Norwich.

Davis, P. H. 1965. *Flora of Turkey and the East Aegean Islands I*. Edinburgh.

Deam, C. C. 1940. *Flora of Indiana*. Indianapolis.

De Candolle, A. P. 1821. *Regni Vegetabilis systema naturale II*. Parisiis.

—— 1824. *Prodromus systematis naturalis regni vegetabilis I*. Parisiis.

Desvaux, N. A. 1814. Coup d'œuil sur la famille des Plantes Crucifères. *Journ. de Bot. 3*, pp. 145–187.

Druce, G. C. 1906. On the nomenclature of British plants as affected by the law adopted by the botanical congress at Vienna. *Ann. Scott. Nat. Hist. 1906*, pp. 217–229.

—— 1925. Additions to the Flora Zetlandica. *Rep. Bot. Soc. Exch. Club Brit. Isles 7*, pp. 628–657.

—— 1928. *British Plant List*. Arbroath.

Dupont, P. 1962. *La Flore Atlantique*. Toulouse.

Ehrendorfer, F. 1959. Differentiation-Hybridization Cycles and Polyploidy in Achillea. *Cold Spring Harbor Symp. Quant. Biol. 24*, pp. 141–152.

—— 1965. Dispersal Mechanisms, Genetic Systems, and Colonizing Abilities in Some Flowering Plant Families. H. G. Baker & G. L. Stebbins (ed.): *The Genetics of Colonizing Species*, pp. 331–351. New York and London.

Ehrhart, F. 1790. Versuch eines Verzeichnisses der um Upsal wild wachsenden Pflanzen 1. *Beitr. Naturkunde 5*, pp. 1–40. Hannover und Osnabrück.

Englund, B. 1942. Die Pflanzenverteilung auf den Meeresufern von Gotland. *Acta Bot. Fenn. 32*. Helsingfors.

Erdtman, G. 1952. *Pollen morphology and plant taxonomy. Angiosperms*. Uppsala.

—— 1958. Über die Pollenmorphologie von Rorippa silvestris. *Flora 146*, pp. 408–411.

—— 1963*a*. *Introduktion till palynologin*. Solna.

—— 1963*b*. Palynology and pleistocene ecology. A. & D. Löve (ed.): *North Atlantic Biota and their History*, pp. 367–375. Norwich.

Eriksson, G. 1962. Elias Fries och den romantiska biologien. *Lychnos-Bibliotek 20*. Uppsala.

Erkamo, V. 1944. Tahmeasta peltovillasta, Senecio viscosus L., ja sen leviämisestä maasamme. *Ann. Bot. Soc. Vanamo 20:2*. Helsinki.

—— 1952. Pienikukkaisesta häpykannuksesta, Impatiens parviflora DC., Suomessa. *Arch. Soc. Vanamo 6*, pp. 87–94.

Fægri, K. 1960. *Maps of distribution of Norwegian vascular plants. Coast plants*. Oslo.

Fagerlind, F. 1937. Embryologische, zytologische und bestäubungsexperimentelle Studien in der Familie Rubiaceae nebst Bemerkungen über einige Polyploiditätsprobleme. *Acta Horti Berg. 11*, pp. 175–470.

Fagerström, L. 1939–40. Ett bidrag till kännedom om vegetation och flora i Terijoki socken på Karelska näset. *Mem. Soc. F. Fl. Fenn. 15*, pp. 94–140.

—— 1942. Roripa austriaca (Crantz) Besser i Terijoki. *Ibid. 17*, pp. 70–72.

—— 1944. Fyra för Öst-Karelen nya adventivväxter. *Ibid. 19*, pp. 137–143.

—— 1945. Växtgeografiska anteckningar från en färd i Fjärr-Karelen sensommaren 1942. *Ibid. 20*, pp. 107–142.

—— 1958. Floristiska anteckningar i Ok 1954–1955. *Ibid. 33*, pp. 37–55.

Fagerström, L. & Luther, H. 1946. Ett bidrag till kännedomen om floran i Vieljärviområdet i Karelia olonetsensis. *Ibid. 21*, pp. 18–45.
Fernald, M. L. 1928. Roripa islandica and R. hispida. *Rhodora 30*, pp. 131–133.
—— 1929. Roripa islandica an invalid Name. *Ibid. 31*, pp. 17–18.
—— 1940. Some Spermatophytes of Eastern North America. *Ibid. 42*, pp. 239–276.
—— 1948. Rorippa: a Correction. *Ibid. 50*, p. 100.
—— 1950. *Gray's Manual of Botany*, ed. 8. New York.
Flora Europaea I, 1964. Cambridge.
Flora Murmanskoy oblasti III, 1956. Moskva and Leningrad.
Florin, M.-B. 1957. Plankton of Fresh and Brackish Waters in the Södertälje Area. *Acta Phytogeogr. Suec. 37*. Uppsala.
Fredskild, B. 1964. Agrostis scabra in Greenland. *Bot. Tidsskr. 60*, pp. 42–46.
Fries, E. 1928. *Novitiae Florae Suecicae*, ed. 2. Londini Gothorum.
—— 1835. *Corpus florarum provincialium Sueciae I. Floram Scanicam scripsit* ... Upsaliae.
—— 1843. *Novitiarum Florae Suecicae Mantissa tertia V.* Upsaliae.
Fries, M. 1948. Limes norrlandicus-studier. En växtgeografisk gränsfråga historiskt belyst och exemplifierad. *Sv. Bot. Tidskr. 42*, pp. 51–69.
Fries, Th. M. 1861. Anteckningar rörande en i Paris befintlig Linneansk växtsamling. *Öfvers. K. Sv. Vet.akad. förh. 18*, pp. 255–272.
Fröhlich, A. 1914. Über den Bastard Roripa austriaca × silvestris und dessen Vorkommen in Mähren. *Österr. bot. Zeitschr. 64*, pp. 120–134.
Garsault, F. A. de 1767. *Description vertus et usages de 719 plantes tant étrangères que de nos climats*. Paris.
Gelmi, E. 1898. Aggiunte alla flora trentina. *Nuovo Giorn. bot. ital. N. S. 5*, p. 305.
—— 1900. Nuove aggiunte alla flora trentina. *Boll. Soc. bot. ital. 1900*, p. 69.
Gerber, C. 1899. Le genre Tetrapoma, sa signification. *C. R. hebd. Soc. Biol. Paris 51, sér. 11*, pp. 665–667.
Glück, H. 1911. *Biologische und morphologische Untersuchungen über Wasser- und Sumpfgewächse 3: Die Uferflora*. Jena.
Godron, D.-A. 1843. *Flore de Lorraine I*. Nancy.
—— 1854. Quelques notes sur la flore de Montpellier. *Mém. Soc. émul. Doubs, sér. 2, 5*. Besançon.
Grande, L. 1926. Rettificazioni ed aggiunte all'Index Kewensis 3. *Bull. ort. bot. Univ. Napoli 8*, pp. 5–144.
Granlund, E. 1930. De geografiska betingelserna för Stockholms uppkomst. *Ymer 50*, pp. 278–301.
Green, P. S. 1955. Pollen Grain Size in Nasturtium and Cakile. *Trans. Proc. Bot. Soc. Edinb. 36*, pp. 289–304.
—— 1962. Watercress in the New World. *Rhodora 64*, pp. 32–43.
Gremli, A. 1867. *Excursionsflora für die Schweiz*. Aarau.
Grenier, C. & Godron, D.-A. 1848. *Flore de France I*. Besançon.
Griffith, J. 1895. *The Flora of Anglesey and Carnavonshire*. Bangor.
Grimm, J. F. C. 1773. Synopseos methodicae stirpium agri Isenacensis ... emendationes et supplementa. *N. Acta phys-med. Acad. Caes. Leopold.-Carol. nat. cur. 5*, pp. 117–160.
Gröntved, J. 1942. *The Pteridophyta and Spermatophyta of Iceland. The Botany of Iceland 4:1*. Köbenhavn.
Grossheim, A. A. 1950. *Flora Kavkaza IV*, ed. 2. Moskva and Leningrad.

Habeler, E. 1963. Cytotaxonomie von Cardamine amara des Alpenostrandes. *Phyton 10*, pp. 161–205.

Håkansson, A. 1948. Syncytiebildning i antererna av Chaerophyllum aureum. *Bot. Notiser 1948*, pp. 425–429.

Haller, A. v. 1742. *Enumeratio methodica stirpium Helvetiae indigenarum*. Goettingae.

—— 1768. *Historia stirpium indigenarum Helvetiae inchoatae I*. Bernae.

Hansen, K. 1966. Vascular Plants in the Faeroes. *Dansk Bot. Arkiv 24:3*. Köbenhavn.

Hanssen, O. & Nordhagen, R. 1930. Die Adventivflora einiger westnorwegischen Kornmühlen in den Jahren 1927–1928. *Bergens Mus. Årbok 1930, Naturvid. rekke, 4*.

Hara, H. 1952. Contributions to the Study of Variations in the Japanese Plants closely related to those of Europe or North America 1. *Journ. Fac. Sci. Univ. Tokyo, Sect. 3, Botany, 6*, pp. 29–96.

Hård av Segerstad, F. 1924. *Sydsvenska florans växtgeografiska huvudgrupper*. Malmö.

—— 1935. Pflanzengeographische Studien im nordwestlichen Teil der Eichenregion Schwedens, 1–2. *Ark. f. Bot. 27 A : 1*. Stockholm.

—— 1952. Den värmländska kärlväxtflorans geografi. *Göteb. K. Vetensk. Vitterh. samh. handl., 6. följd., ser. B, 7*. Göteborg.

Hartman, C. J. 1879. *Handbok i Skandinaviens flora*, ed. 11. Stockholm.

Hasselrot, K. 1967. *Västergötlands flora*. Lund.

Hayek, A. v. 1911. Entwurf eines Cruciferen-Systems auf phylogenetischer Grundlage. *Beih. Bot. Centralbl. 27*, pp. 127–335.

—— 1924–27. Prodromus Florae peninsulae Balcanicae I. *Feddes Repertorium (Beih.) 30:1*.

Häyrén, E. 1909. Björneborgstraktens vegetation och kärlväxtflora. *Acta Soc. F. Fl. Fenn. 32:1*. Helsingforsiae.

Hedberg, I. 1961. Cytotaxonomic studies in Anthoxanthum odoratum L. s.lat. I. Morphologic analysis of herbarium specimens. *Sv. Bot. Tidskr. 55*, pp. 118–128.

—— 1967. Cytotaxonomic studies on Anthoxanthum odoratum L. s.lat. II. Investigations of some Swedish and of a few Swiss population samples. *Symb. Bot. Upsal. 18:5*. Uppsala.

Hedberg, O. 1957. Afroalpine Vascular Plants. *Symb. Bot. Upsal. 15:1*. Uppsala.

Hegi, G. 1958–63. *Illustrierte Flora von Mittel-Europa 4:1*. Ed. 2 (ed. F. Markgraf). München.

Heslop-Harrison, J. 1953. The North American and Lusitanian elements in the flora of the British Isles. J. E. Lousley (ed.): *The Changing Flora of Britain*, pp. 105–123. Arbroath.

Heukels, H. & Ooststroom, S. J. van 1956. *Flora van Nederland*, 14th print. Groningen.

Hiitonen, I. 1947. Für die Flora Finnlands neue Phanerogamen aus der Stadt Helsinki nebst Erörterung einiger Rorippa-Formen. *Mem. Soc. F. Fl. Fenn. 23*, pp. 181–185.

Hjelt, H. 1904–06. Conspectus floræ fennicae 3:2. Caryophyllaceae-Resedaceae. *Acta Soc. F. Fl. Fenn. 30:1*. Helsingfors.

Holmgren, B. 1942. *Blekinges flora*. Karlshamn.

Howard, H. W. 1946. Chromosome Number of Rorippa (Nasturtium) sylvestris. *Nature 158*, p. 666.

—— 1947*a*. Seed size in crosses between diploid and autotetraploid Nasturtium officinale and allotetraploid Nasturtium uniseriatum. *Journ. Genet. 48*, pp. 111–118.
—— 1947*b*. Wild and cultivated watercress types. *Agriculture 53*, pp. 453–456.
—— 1947*c*. Chromosome Numbers of British species of the genus Rorippa Scop. (part of the genus Nasturtium R. Br.). *Nature 159*, pp. 66–67.
Howard, H. W. & Lyon, A. G. 1950. The Identification and Distribution of the British Watercress Species. *Watsonia 1*, pp. 228–233.
Howard, H. W. & Manton, I. 1946. Autopolyploid and allopolyploid watercress with the description of a new species. *Ann. of Bot. N. S. 10*, pp. 1–13.
Hultén, E. 1928. Flora of Kamtchatka and the adjacent islands II. *K. Sv. Vet. akad. handl., ser 3, 5:2*. Uppsala.
—— 1937*a*. *Flora of the Aleutian Islands*. Stockholm.
—— 1937*b*. *Outline of the History of Arctic and Boreal Biota during the Quaternary Period*. Stockholm.
—— 1945. Flora of Alaska and Yukon V. *Lunds univ. årsskr. N. F. avd. 2, 41:1*, and *K. Fysiograf. Sällsk. handl. N. F. 56:1*. Lund.
—— 1946. *Schedae operis quod inscribitur G. Samuelsson: Plantae Sueciae Exsiccatae*. Falköping.
—— 1950. *Atlas över växternas utbredning i Norden*. Stockholm.
Hyde, H. A. & Wade, A. E. 1957. *Welsh Flowering Plants*, ed. 2. Cardiff.
Hylander, N. 1938. Om bondpionens uppkomst och vetenskapliga namn. *Lustgården 18–19*, pp. 69–76. Stockholm.
—— 1943*a*. Die Grassameneinkömmlinge schwedischer Parke. *Symb. Bot. Upsal. 7:1*. Uppsala.
—— 1943*b*. Thlaspi alpestre L. i Sverige. *Sv. Bot. Tidskr. 37*, pp. 377–402.
—— 1945. Nomenklatorische und systematische Studien über nordische Gefässpflanzen. *Uppsala univ. årsskr. 1945:7*. Uppsala.
—— 1950. Rorippa microphylla i Sverige och Danmark. *Bot. Notiser 1950*, pp. 1–13.
—— 1953. *Nordisk kärlväxtflora I*. Uppsala.
—— 1960. Rorippa amphibia funnen vildväxande i norra Österbotten. *Sv. Bot. Tidskr. 54*, pp. 273–275.
—— 1961. Rorippa amphibia × islandica funnen i norra Finland. *Mem. Soc. F. Fl. Fenn. 37*, pp. 253–255.
—— 1966. *Nordisk kärlväxtflora II*. Uppsala.
International Code of Botanical Nomenclature, 1966. Ed. 5. *Regnum vegetabile 46*. Utrecht.
Iversen, J. 1952. Origin of the flora of western Greenland in the light of pollen analysis. *Oikos 4*, pp. 85–103.
Jaakkola, J. 1933*a*. Finlands handel och sjöfart under tidigare medeltiden. *Nordisk Kultur 16*, pp. 167–180. Köbenhavn.
—— 1933*b*. Finlands vägar och samfärdsleder under medeltiden. *Ibid.* pp. 256–265.
Jackson, B. D. 1912. Index to the Linnaean herbarium. *Suppl. Proc. Linn. Soc. 124th Session*. London.
—— 1928. *A Glossary of Botanic terms*, ed. 4. London.
Jalas, J. 1965. *Suuri kasvikirja II*. Helsingissä.
Janchen, E. 1942. Das System der Cruciferen. *Österr. bot. Zeitschr. 41*, pp. 1–28.
—— 1956–60. *Catalogus Florae Austriae I. Pteridophyta und Anthophyten*. Wien.

JARETZKY, R. 1928. Untersuchungen über Chromosomen und Phylogenie bei einigen Cruciferen. *Jahrb. wiss. Bot. 68*, pp. 1–45.

—— 1932. Beziehungen zwischen Chromosomenzahl und Systematik bei der Cruciferen. *Ibid. 76*, pp. 485–527.

JOHANSSON, K. 1897. Hufvuddragen af Gotlands växttopografi och växtgeografi. *K. Sv. Vet.akad. handl. 29:1.* Stockholm.

JONES, E. W. 1937. The Vegetation of Grímsey, Iceland. *Journ. Ecol. 25*, pp. 222–253.

JONES, G. N. & FULLER, G. D. 1955. *Vascular plants of Illinois.* Urbana.

JONSELL, B. 1963. On Rorippa × sterilis in Sweden. *Bot. Notiser 116*, pp. 1–6.

—— 1964. Chromosome numbers of Rorippa silvestris (L.) Bess. in Scandinavia. *Sv. Bot. Tidskr. 58*, pp. 204–208.

JÖRGENSEN, C. A., SÖRENSEN, T. & WESTERGAARD, M. 1958. The flowering plants of Greenland. *Biol. Skr. K. Dan. Vidensk. Selsk. 9:4.* Köbenhavn.

JULIN, E. & PEKKARI, S. 1965. The north-east corner. *Acta Phytogeogr. Suec. 50*, pp. 205–214. Uppsala.

KALELA, A. 1943. Die Ostgrenze Fennoskandiens in pflanzengeographischer Beziehung. *Veröff. geobot. Inst. Rübel 20.* Bern.

KELLER, J. 1943. De originalibus Crantzianis. *Ann. hist.nat. Mus. nat. Hung., pars bot. 36*, pp. 95–128.

KINDBERG, N. C. 1901. *Östgöta flora*, ed. 4. Stockholm.

KOPECKÝ, K. 1965*a*. Einfluss der Ufer- und Wassermakrophyten-Vegetation auf die Morphologie des Flussbettes einiger tschechoslowakischer Flüsse. *Arch. Hydrobiol. 61*, pp. 137–160.

—— 1965*b*. Zur Ökologie der Makrophyten an Flussufern. *Preslia 37*, pp. 246–263.

LAGERKRANZ, J. 1950. Observations on the Flora of West and East Greenland. *N. Acta R. Soc. Sci. Upsal. Ser. 4, 14:6.* Uppsala.

LAKELA, O. 1948. A prostrate Rorippa in the Interior. *Rhodora 50*, p. 132.

—— 1965. *A Flora of Northeastern Minnesota.* Minneapolis.

LANGE, J. 1880. Conspectus florae groenlandicae. *Medd. om Grönland 3.* Kjöbenhavn.

LANJOUW, J. & STAFLEU, F. A. 1964. Index herbariorum I. The herbaria of the world, ed. 5. *Regnum vegetabile 31.* Utrecht.

LARSEN, A. 1956. Bornholms flora. *Bot. Tidsskr. 52*, pp. 189–316.

LARSEN, K. 1956. Chromosome Studies in Some Mediterranean and South European Flowering Plants. *Bot. Notiser 109*, pp. 293–307.

LARSSON, L. M. 1868. *Flora öfver Wermland och Dal*, ed. 2. Carlstad.

LASÈGUE, A. 1845. *Musée botanique de M. Benjamin Delessert.* Paris.

LAWALRÉE, A. 1955–57. *Flore générale de Belgique. Spermatophytes II.* Bruxelles.

LEDEBOUR, C. F. 1842. *Flora Rossica I.* Stuttgartae.

LID, J. 1963. *Norsk og svensk flora.* Oslo.

LIDMAN, G. 1925. Några anteckningar om Hälsinglands flora. *Sv. Bot. Tidskr. 19*, pp. 84–97.

LILJA, N. 1870. *Skånes flora*, ed. 2. Stockholm.

LINDBERG, H. 1958. Växter kända från Norden i Linnés herbarium. *Acta Bot. Fenn. 20.* Helsingfors.

LINDERS, J. 1946. Cyperus fuscus vid Vombsjön. *Bot. Notiser 1946*, p. 124.

LINDROTH, C. 1963. The problem of late land connections in the North Atlantic area. A. & D. LÖVE (ed.): *North Atlantic Biota and their History*, pp. 73–85. Norwich.

Linkola, K. 1916, 1921. Studien über den Einfluss der Kultur auf die Flora in den Gegenden nördlich vom Ladogasee I–II. *Acta Soc. F. Fl. Fenn. 45.* Helsingfors.
Linnaeus, C. 1737*a*. *Flora Lapponica*,.. Amstelaedami.
—— 1737*b*. *Hortus Cliffortianus*,.. Amstelaedami.
—— 1745. *Flora Suecica*. Stockholmiae.
—— 1753. *Species Plantarum*. Holmiae.
—— 1755. *Flora Suecica*, ed. 2. Stockholmiae.
—— 1756. Herbationes Upsalienses. *Amoenitates academicae III*. Holmiae.
Löve, A. 1954. Cytotaxonomical evaluation of corresponding taxa. *Vegetatio. Acta geobot. 5–6*, pp. 212–224. Den Haag.
Löve, A. & Löve D. 1956. Cytotaxonomical Conspectus of the Icelandic Flora. *Acta Hort. Gotoburg. 20*, pp. 65–290.
—— 1961. Chromosome numbers of Central and Northwest European Plant Species. *Opera botanica 5*. Lund.
Löve, D. 1963. Dispersal and survival of plants. A. & D. Löve (ed.): *North Atlantic Biota and their History*, pp. 189–205. Norwich.
Lövkvist, B. 1956. The Cardamine pratensis complex. *Symb. Bot. Upsal. 14:2*. Uppsala.
Lundqvist, G. 1930. Drag ur Stockholmstraktens hydrografi. *Ymer 50*, pp. 221–242.
Luther, H. 1948–49. Krigets spår i Finlands flora. *Mem. Soc. F. Fl. Fenn. 24*, pp. 138–160.
Magnusson, N. H., Lundqvist, G. & Regnéll, G. 1963. *Sveriges geologi*, ed. 4. Stockholm.
Mäkinen, Y. & Laine, U. 1962. Turun tulokaskasvisto I. *Publ. Dep. Bot. Univ. Turku 31*. Forssa.
Mannerkorpi, P. 1944–45. Uhtuan taistelurintamalle saapuneista tulokaskasveista. *Ann. Bot. Soc. Vanamo 20*. Notulae pp. 39–51. Helsinki.
Mansfeld, R. 1938. Zur Nomenklatur der Farn- und Blütenpflanzen Deutschlands. *Feddes Repertorium 44*, pp. 285–322.
—— 1939. Do. IV. *Ibid. 46*, pp. 97–121.
Manton, I. 1932. Cytology of the Cruciferae. *Ann. of Bot. 46*, pp. 509–556.
—— 1934. The problem of Biscutella laevigata L. *Zeitschr. ind. Abst. Vererb.lehre 67*, pp. 41–57. Leipzig.
—— 1937. Do. II. The Evidence from Meiosis. *Ann. of Bot. N. S. 1*, pp. 438–462.
Marie-Victorin, F. 1930. Le genre Rorippa dans le Québec. *Contr. Lab. Bot. Univ. Montréal 17*. Montréal.
Mathiasson, S. 1958. Fåglar kring Vombsjön. *Skånes Natur 45*, pp. 58–90.
Maurizio, A. 1956. Pollengestaltung bei einigen polyploiden Kulturpflanzen. *Grana palynol. N. S. 1*, pp. 59–69.
Metcalfe, C. R. & Chalk, L. 1950. *Anatomy of the Dicotyledons I*. Oxford.
Meusel, H., Jäger, E. & Weinert, E. 1965. *Vergleichende Chorologie der zentraleuropäischen Flora*. Jena.
Moench, K. 1794. *Methodus plantas horti botanici et agri Marburgensis a staminum situ describendi*. Marburgi Cattorum.
Mulligan, G. A. 1964. Chromosome numbers of the family Cruciferae I. *Canad. Journ. Bot. 42*, pp. 1509–1519.
—— 1965. Do. II. *Ibid. 43*, pp. 657–668.
—— 1966. Do. III. *Ibid. 44*, pp. 309–319.
Müntzing, A. 1933. Apomictic and sexual seed formation in Poa. *Hereditas 17*, pp. 131–153.

Murley, M. R. 1951. Seeds of the Cruciferae of Northeastern North America. *Amer. Midl. Nat. 46*, pp. 1–81.

Murr, J. 1897. Beiträge zur Flora von Tirol und Vorarlberg IX. *Dtsch. bot. Monatsschr. 15*, pp. 76–81.

—— 1899. Do. XI. *Ibid. 17*, p. 13.

Murray, J. A. 1773. Observationes super stirpibus quibusdam recens inventis et raribus in horto academico institutae. *N. Comm. Soc. r. sci. Gotting. 3*, pp. 60–84.

Neilreich, A. 1852. Über hybride Pflanzen der Wiener Flora. *Verh. zool. bot. Vereins Wien 1*, pp. 114–131.

Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. *Handbuch der Pflanzenanatomie 2. Abt., 2. Teil, Bd X*. Berlin.

Neuman, L. M. & Ahlfvengren, F. 1901. *Sveriges Flora (Fanerogamerna)*. Lund.

Nordman, C. A. 1933. Finlands handel med Skandinavien under forntiden. *Nordisk Kultur 16*, pp. 68–86. Köbenhavn.

Nordstedt, O. 1920. Prima loca plantarum suecicarum. *Suppl. Bot. Notiser 1920*. Lund.

Norman, J. 1894–95. *Norges arktiske flora I–II*. Kristiania.

Oeder, G. C. 1768. *Flora Danica III*. Havniae.

Ostenfeld, C. H. 1926. The Flora of Greenland and its Origin. *K. Dansk. Vidensk. Selsk. biol. Medd. 6:3*. Köbenhavn.

Ouren, T. 1959. Om skipsfartens betydning for Norges flora. *Blyttia 17*, pp. 96–118.

Patman, J. & Iltis, H. H. 1961. Preliminary reports on the flora of Wisconsin 44. Cruciferae — Mustard Family. *Trans. Wisc. Acad. 50*, pp. 17–72.

Pedersen, A. 1958. Cruciférernes udbredelse i Danmark. *Bot. Tidsskr. 54*, pp. 191–304.

—— 1965. Adventivfloraen i Ivigtut og Grönnedal. *Bot. Tidsskr. 61*, pp. 88–97.

Perrier de la Bathie, E. 1917. Catalogue raisonné des plantes vasculaires de Savoie. *Mém. Acad. sci. b.-l. arts Savoie 5:4*. Chambéry.

Perring, F. H. & Walters, S. M. 1962. *Atlas of the British Flora*. Norwich.

Pettersson, B. 1958. Dynamik och konstans i Gotlands flora och vegetation. *Acta Phytogeogr. Suec. 40*. Uppsala.

Pohjala, L. 1934. Kokemäen pitäjän kasvisto. *Ann. Bot. Soc. Vanamo 5:3*. Helsinki.

Pollich, J. A. 1777. *Historia plantarum in Palatinatu electorali sponte crescentium incepta,.. II*. Mannhemii.

Polunin, N. 1959. *Circumpolar Arctic Flora*. Oxford.

Porsild, A. E. 1945. A survey of the adventitious flora of Ivigtut in Southwest Greenland. *Canad. Field-Nat. 59*, pp. 53–59.

—— 1951. Botany of southeastern Yukon adjacent to the Canol Road. *Bull. Nat. Mus. Canada 121*. Ottawa.

Porsild, M. P. 1932. Alien plants and apophytes of Greenland. *Medd. om Grönland 92:1*. Köbenhavn.

Praeger, R. L. 1909. *A Tourist's Flora of the West of Ireland*. Dublin.

Prodan, G. 1919. Egy új Nasturtium-fajvegülék a Bácskából. *Ungar. bot. Blätter 17*, p. 97.

Raj, B. 1965. Chromosome numbers in some Indian angiosperms II. *Proc. Indian Acad. Sciences, Sect. B, 61*, pp. 253–261.

Raunkiær, C. 1907. *Planterigets Livsformer og deres Betydning for Geografien*. Kjöbenhavn og Kristiania.

Raup, H. M. 1947. The Botany of southwestern Mackenzie. *Sargentia 6*, pp. 1–262.

Rechinger, K. H. 1960. Zur Flora von Syrien, Libanon und den angrenzenden türkischen Gebieten. Reliquiae Samuelssonianae VI. *Ark. f. Bot., ser. 2, 5.* Stockholm.

Reese, G. 1954. Euploidie, Aneuploidie und B-Chromosomen bei Caltha palustris L. *Planta 44*, pp. 203–268.

Regel, E. 1861. Tentamen Florae Ussuriensis. *Mém. Acad. imp. sci. St.-Pétersbourg, sér. 7, 4:4.*

Reichenbach, L. 1830–32. *Flora germanica excursoria.* Dresden.

—— 1837–38. *Icones Florae Germanicae et Helveticae II.* Lipsiae.

Rendle, A. B. 1923. George Clifford's herbarium and the 'Hortus Cliffortianus'. *Journ. of Bot. 61*, pp. 114–116.

Rikli, M. 1903. Die Anthropochoren und der Formenkreis des Nasturtium palustre DC. *Ber. zürch. bot. Ges. 8*, pp. 1–12.

Rollins, R. C. 1941. A monographic study of Arabis in western North America. *Rhodora 43*, pp. 288–325, 348–411, 425–481.

—— 1961. Notes on American Rorippa (Cruciferae). *Ibid. 63*, pp. 1–10.

—— 1966. Chromosome numbers of Cruciferae. *Contr. Gray herb. Harvard univ. 197*, pp. 43–65.

Rosén, E. 1749. *Observationes botanicae circa plantas quasdam Scaniae ... hucusque non detectas*,.. Londini Gothorum.

Rothmaler, W. 1963. *Exkursionsflora von Deutschland*, ed. 4. Leipzig.

Rouy, G. & Foucaud, J. 1895. *Flore de France II.* Tours.

Saarisalo-Taubert, A. 1963. Die Flora in ihrer Beziehung zur Siedlung und Siedlungsgeschichte in den südfinnischen Städten Porvoo, Loviisa und Hamina. *Ann. Bot. Soc. Vanamo 35:1.* Helsinki.

Sahlén, A. J. 1854. *Wenersborgs flora.* Mariestad.

Salisbury, E. 1961. *Weeds and Aliens.* London and Glasgow.

Salomonsen, F. 1950. *Grönlands Fugle.* Köbenhavn.

Samuelsson, G. 1934. Die Verbreitung der höheren Wasserpflanzen in Nordeuropa (Fennoskandien und Dänemark). *Acta Phytogeogr. Suec. 6.* Uppsala.

Santesson, R. 1966. Cladonia sylvatica and the descriptive method of Linnaeus. *Taxon 15*, pp. 64–66.

Säve, C. 1837. *Synopsis florae gothlandicae.* Upsaliae.

Savulescu, T. 1955. *Flora Republicii Populare Romîne III.* București.

Scheerer, H. 1939. Chromosomenzahlen aus der Schleswig-Holsteinischen Flora I. *Planta 29*, pp. 636–642.

Schinz, H. & Thellung, A. 1909. Begründung vorzunehmender Namensänderungen an der zweiten Auflage der „Flora der Schweiz" von Schinz und Keller. *Viertelj.schr. naturf. Ges. Zürich 53*, pp. 493–593.

—— 1913. Weitere Beiträge zur Nomenklatur der Schweizerflora IV. *Ibid. 58*, pp. 35–159.

Schroeter, C. 1908. *Das Pflanzenleben der Alpen.* Zürich.

Schulz, O. E. 1936. Cruciferae. A. Engler & K. Prantl: *Die natürlichen Pflanzenfamilien 17 b.* Ed. 2, pp. 227–658.

Schweidler, J. H. 1911. Über den Grundtypus und die systematische Bedeutung der Cruciferen-Nektarien I. *Beih. Bot. Centralbl. 27*, pp. 337–390.

Scopoli, J. 1760. *Flora Carniolica.* Viennae.

Scully, R. W. 1916. *Flora of County Kerry.* Dublin.

Selander, S. 1950. Floristic Phytogeography of South-Western Lule Lappmark (Swedish Lapland) I. *Acta Phytogeogr. Suec. 27.* Uppsala.

Sernander, R. 1901. *Den skandinaviska vegetationens spridningsbiologi.* Uppsala.
Simmons, H. G. 1910. *Floran och vegetationen i Kiruna.* Lund.
Sjöstrand, M. G. 1863. *Calmar läns och Ölands flora.* Calmar.
Skult, H. 1961. Om kärlväxtfloran i Korpo, Brunskär, en utskärsarkipelag. *Acta Soc. F. Fl. Fenn. 76*, pp. 1–101.
Skårman, J. A. O. 1942. Floristiska undersökningar i trakterna av Anten och Mjörn. *Sv. Bot. Tidskr. 36*, pp. 312–372.
Snogerup, S. 1967. Studies in the Aegean Flora VIII. Erysimum Sect. Cheiranthus. A. Taxonomy. *Opera botanica 13.* Lund.
Snow, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. *Stain Technol. 38*, pp. 9–13.
Solms-Laubach, H. 1900. Cruciferenstudien I. Capsella Heegeri Solms., eine neu entstandene Form des deutschen Flora. *Bot. Zeitung 58*, pp. 167–190.
Soó, R. 1966. Species et combinationes novae florae Europae praecipue Hungariae V. *Acta bot. Acad. scient. Hung. 12*, pp. 355–367.
Sprague, T. A. 1930. The Source of the Generic Name Rorippa. *Journ. of Bot.* 68, p. 219.
—— 1939. Rorippa islandica (Oeder) Borbás. *Ibid. 77*, pp. 343–345.
Stearn, W. T. 1957. An Introduction to the Species Plantarum and cognate botanical works of Carl Linnaeus. Carl Linnaeus: *Species Plantarum. A Facsimile of the first edition 1753 I.* London.
Stebbins, G. L. 1950. *Variation and Evolution in Plants.* New York.
Stefánsson, S. 1948. *Flóra Íslands*, ed. 3. Akureyri.
Steindórsson, S. 1962. On the age and immigration of the Icelandic flora. *Soc. scient. Isl. 35.* Reykjavík.
—— 1963. Ice Age refugia in Iceland as indicated by the present distribution of plant species. A. & D. Löve (ed.): *North Atlantic Biota and their History*, pp. 303–320. Norwich.
Sterner, R. 1938. Flora der Insel Öland. *Acta Phytogeogr. Suec. 9.* Uppsala.
Steyermark, J. A. 1963. *Flora of Missouri.* Nijmegen.
Stuckey, R. L. 1965. The taxonomy and distribution of the genus Rorippa (Cruciferae) in North America (Extract). *Diss. Abstracts 26:6.*
—— 1966*a*. The distribution of Rorippa sylvestris (Cruciferae) in North America. *Sida 2*, pp. 361–376.
—— 1966*b*. Rorippa walteri and R. obtusa synonyms of R. teres (Cruciferae). *Ibid.* pp. 409–418.
Sundqvist, N. 1953. *Uppsala stads historia I. Östra Aros.* Uppsala.
Suominen, J. 1962. Karkua pitäjän putkilokasvisto. *Ann. bot. Soc. Vanamo 32:2.* Helsinki.
Sylvén, N. 1915. Torneträskområdets adventivflora. *Ark. f. Bot. 14:11.* Stockholm.
Tambs Lyche, R. 1931. Adventivfloraen i Buvik. *K. Norske Vidensk.selsk. Skr. 1931:2.* Trondheim.
Tausch, J.-F. 1840. Ueber die in Böhmen vorkommenden, zu Brachylobos gehörigen Arten von Nasturtium. *Flora 45*, pp. 706–718.
Thórarinsson, S. 1937. Vatnajökull. Scientific results of the Swedish-Icelandic investigations 1936–37. II. The Main Geological and Topographical Features of Iceland. *Geogr. Annaler 19*, pp. 161–175.
Timbal-Lagrave, E. 1856. Observations critiques et synonymiques sur l'herbier Chaix. *Mém. Acad. imp. sci. inscr. b.l. Toulouse. Sér. 4, 6*, pp. 85–154.

Tournefort, J. P. de 1719. *Institutiones rei herbariae*, ed. 3. Parisiis.

Turrill, W. B. 1931. Rorippa pyrenaica and closely related species. *Bull. Soc. bot. Bulg. 4*, pp. 48–56.

Tzvelev, N. 1957. Noviy vid roda Rorippa Scop. (Species nova generis Rorippa Scop.). *Bot. materialy 18*, pp. 98–100. Leningrad.

Vaillant, S. 1727. *Botanicon Parisiense*. Leide et Amsterdam.

Valovirta, E. J. & Segerstråle, S. G. 1956. Data on the nature of Finland. S. G. Segerstråle (ed.): *Limnologorum Conventus 13*, pp. 3–49. Helsinki.

Velenovský, J. 1883. O medových zlázkách rostlin krízatých a jich upotrebené v systematice radu tohoto. *Abh. mat. nat. Cl. K. böhm. Ges. Wissensch., VI Folge, 12*.

Villani, A. 1912. Dei nettarii di alcune specie di Nasturtium (L.) R. Br. *Nuovo Giorn. bot. ital. 19*, pp. 499–506.

Villar(s), D. 1785. Flora delphinalis. In J. E. Gilibert: *Caroli Linnaei Systema plantarum I*. Coloniae Allobrogum.

—— 1789. *Histoire des plantes du Dauphiné III*. Grenoble.

Wahlenberg, G. 1820. *Flora Upsaliensis enumerans plantas circa Upsaliam sponte crescentes*. Upsaliae.

—— 1821. Gothlandiae plantae rariores. *N. Acta Soc. Scient. Ups. 8*, pp. 203–257.

—— 1824. *Flora Suecica I*. Upsaliae.

Wallén, A. 1911. Kännedomen om Sveriges hydrografi före tiden omkring år 1870. *Hydrografiska byråns årsbok 1908*. Stockholm.

Wallroth, F. W. 1822. *Schedulae criticae de plantis florae halensis selectis*. Halae.

—— 1840. Scholion zu Hampe's Prodromus Florae Hercyniae. *Linnaea 14*, pp. 1–158, 529–727.

Weimarck, H. 1958. Bidrag till Skånes Flora 52. Utforskningen av Skånes flora. *Bot. Notiser 111*, pp. 81–122.

—— 1963. *Skånes flora*. Lund.

Wiggins, I. L. & Thomas, J. H. 1962. *A Flora of the Alaskan Arctic Slope*. Toronto.

Willén, T. 1962. The Utål Lake Chain, Central Sweden and its Phytoplankton. *Oikos suppl. 5*. Odense.

Wilson, C. L. 1927. Adventitious roots and shoots in an introduced weed. *Bull. Torr. Bot. Cl. 54*, pp. 35–38.

Winge, Ö. 1933. A Case of Amphidiploidy within the Collective Species Erophila verna. *Hereditas 18*, pp. 181–191.

—— 1940. Taxonomic and evolutionary studies in Erophila based on cytogenetic investigations. *C. R. trav. Lab. Carlsberg. Sér. physiol. 23*, pp. 41–78.

Wittrock, V. B. 1884. Om rotskott hos örtartade växter, med särskild hänsyn till deras olika biologiska betydelse. (ref. of lecture). *Bot. Notiser 1884*, pp. 21–37.

Wulff, H. D. Chromosomenstudien an der schleswig-holsteinischen Angiospermen-Flora III. *Ber. dtsch. bot. Ges. 57*, pp. 84–91.

Zapałowicz, H. 1913. Krytyczny przeglad roślinności Galicyi XXIV. *Bull. int. Acad. sci. Cracov. Cl. sci. mat. nat. Sér. B: Sci. nat. A. 1912*, pp. 345–348.

Zbořil, J. 1922. Vegetativní množení drůhu Roripa amphibia a Sagittaria sagittaefolia. *Mém. Soc. R. Sci. Bohême. Cl. sci. 1920:4*. Prague.

Zinger, V. J. 1885. *Sbornik svedeniy o flore Sredney Rossii*. Moskva. (Non vidi.)

Zschacke, H. 1901. Beiträge zur Flora Anhaltina VIII, 2. Stück. *Dtsch. bot. Monatsschr. 19*, pp. 72–74.

EXPLANATION OF PLATES

Plate I. A–F. Somatic metaphases in sections of root-tips, all c. 1700 × (A. *R. islandica*, $2n = 16$ (J 681). B. Progeny of back-cross of *R. austriaca* × *sylvestris* to *R. sylvestris*, $2n = 31$ (J 541 × J 870). C. *R. sylvestris*, $2n = 32$ (J 900). D. *R. sylvestris*, $2n = 33$ (J 1135a). E. *R. sylvestris*, $2n = 40$ (J 865). F. *R. sylvestris*, $2n = 48$ (J 878). G. Metaphase I in PMC of progeny, $2n =$ c. 44, of a cross within *R. sylvestris* (J 401 × J 357), 1200 ×. H. Metaphase I in PMC of progeny, $2n = 48$, of a cross within *R. sylvestris* (J 531 × J 188) showing some probable univalents outside the plate, 1300 ×. I. Telophase I in the same plant as in H, 1200 ×. J. Metaphase II in PMC of an artificial *R. amphibia* × *palustris* hybrid, $2n = 32$ (J 379 × J 471), with one lagging, divided chromosome, 1400 ×. K. Apparently regular metaphases II—telophases II in the same plant as in J, 1100 ×.

Plate II. A. Tricolpate pollen grain of *R. sylvestris*, (J 1129). B. Tricolpate pollen grain of *R. austriaca* × *sylvestris*, (J 1220). C. Tetracolpate pollen grains of *R. sylvestris* (J 188). D. Pancolpate pollen grain of *R. sylvestris* (J 188). E. Nonaperturate, perforate pollen grain of *R. sylvestris* (J 171). D. Nonaperturate pollen grain of *R. sylvestris* (J 143). All 1100 ×.

Plate III. A–C. Cross-sections of pollen grains, 1500 × A. Tri- and tetracolpate grains of *R. austriaca* × *sylvestris* (J 1220). B. Nonaperturate, perforate grains of *R. sylvestris* (J 1234). C. Nonaperturate grains of *R. sylvestris* (J 171). D. PMCs of *R. sylvestris* with nonaperturate pollen irregularly and incompletely divided into dyads, 750 × (J 186). E. PMC (at different foci) of *R. sylvestris* with nonaperturate pollen divided into a tetrad, around which a wall is beginning to be formed, 1800 × (J 1113). F–G. Cross-sections of pod-valves (inner side downwards), 200 × (F: *R. islandica* (J 944). G: *R. palustris* (J 350)).

Plate IV. Cross-sections of seed-coats showing the prominent outer seed-epidermis, 280 × (A, C, E, G) and tangential sections of the outer seed-epidermis, 460 × (B, D, F, H). A–B. *R. islandica* ssp. *islandica* (1934 Taylor, BM). C–D. *R. islandica* ssp. *dogadovae* (Pavlov No. 33, LE). E–H. *R. palustris* (E–F: J 369. G: J 175. H: J 142).

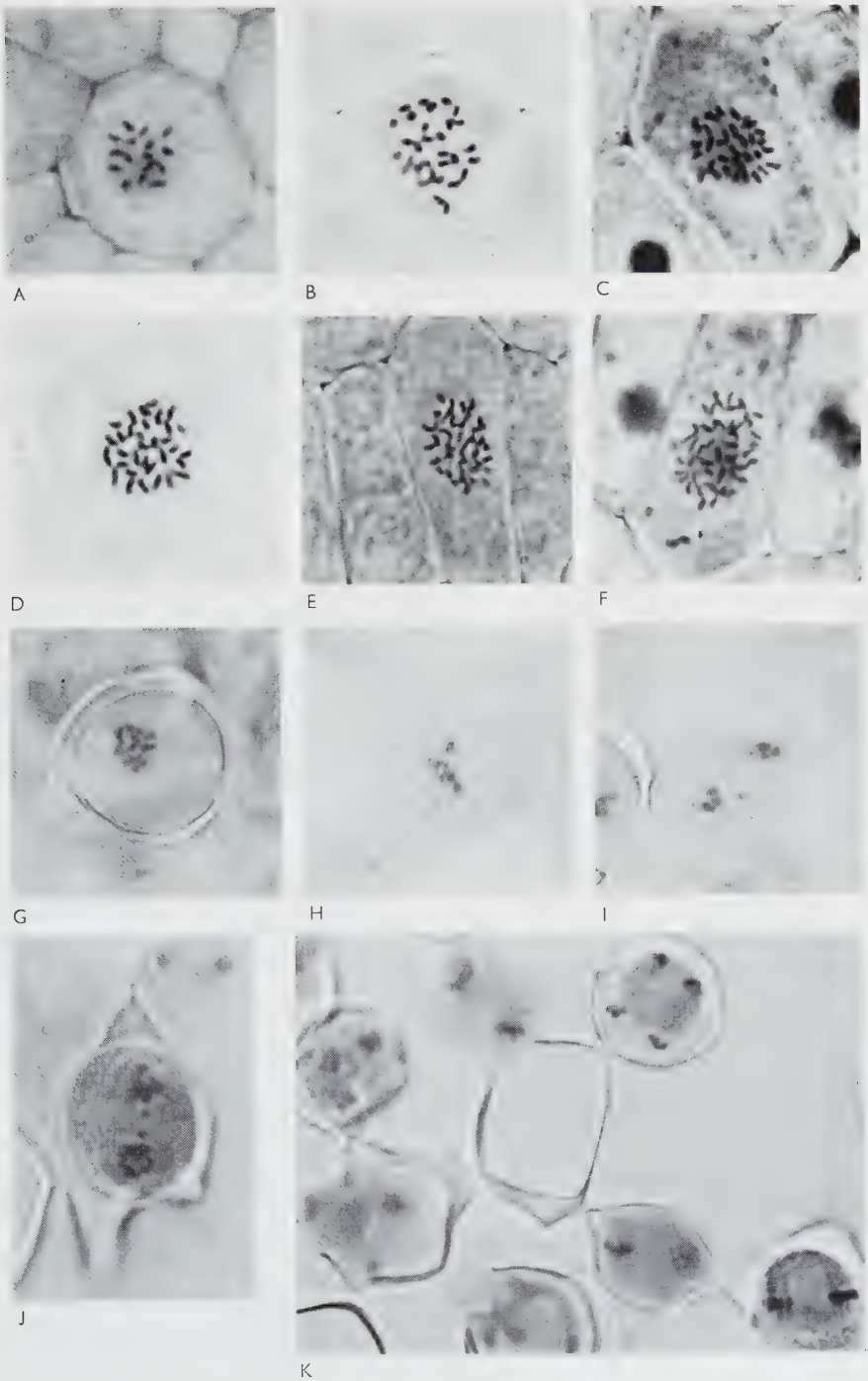
Plate V. A. Ripe pods of *R. islandica*, c. 5 × (J 977). B. Ripe pods of a short-fruited specimen of *R. palustris* c. 5 × (J 1456). C. *R. islandica* branching from the base into decumbent stems, c. 0.3 × (J 672). D. *R. islandica* with a decumbent floral stem branched in approximately one plane, c. 0.3 × (J 721). E. *R. palustris* with markedly erect stem, c. 0.2 × (J 509). F. *R. palustris*, a number of fairly erect plants, c. 0.2 × (J 1572).

Plate VI. *R. amphibia* × *sylvestris*. Shoot of a cultivated tetraploid plant from L. Mälaren (J 920). c. 0.4 ×.

Plate VII. *R. amphibia* × *sylvestris*. Shoot of a cultivated pentaploid plant from L. Vombsjön (J 536). c. 0.4 ×.

Plate VIII. *R. amphibia* × *palustris*. Shoot of a tetraploid plant, progeny of the cross J 379 × J 471. c. 0.4 ×.

Plates IX–XI. *R. sylvestris*. Shoots of clones representing extremes of the Scandinavian variation range, all from plants in cultivation. *Plate IX*: Hexaploids with nonaperturate pollen from Finland (J 1113, to the left) and Denmark (J 886, to the right) probably belonging to the same clone. c. 0.4 ×. *Plate X*: Short but vigorous shoots of a hexaploid with colpate pollen (J 1254). c. 0.5 ×. *Plate XI*: Tetraploid shore form from L. Mälaren (J 918) in flower and with ripe pods. c. 0.4 ×.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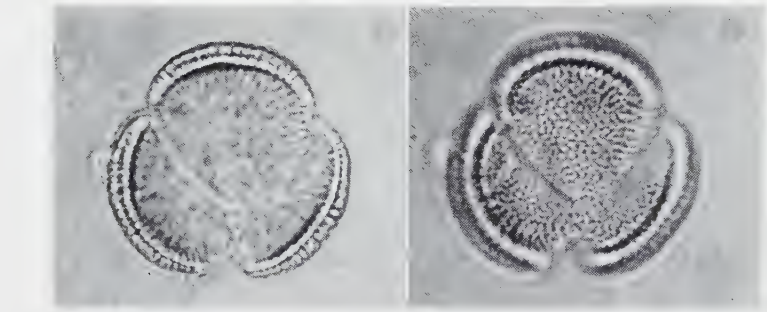

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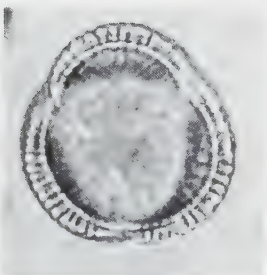

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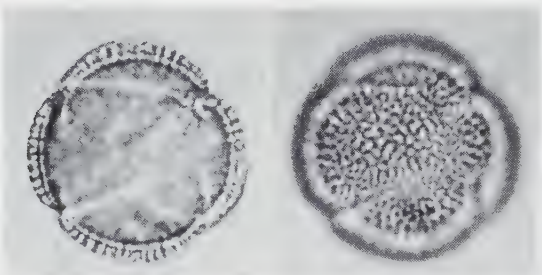

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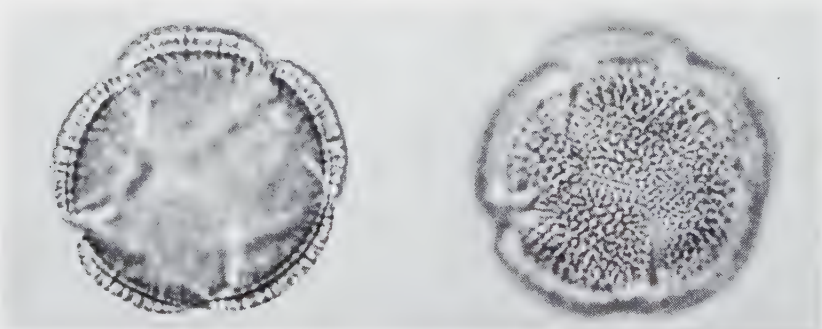

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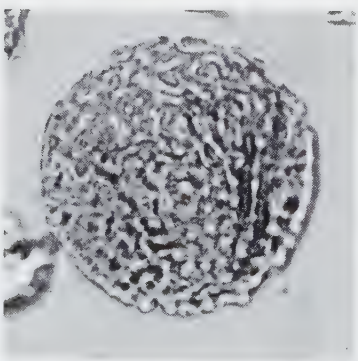

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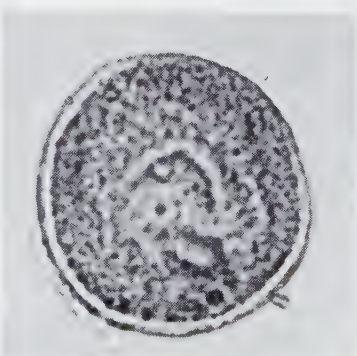

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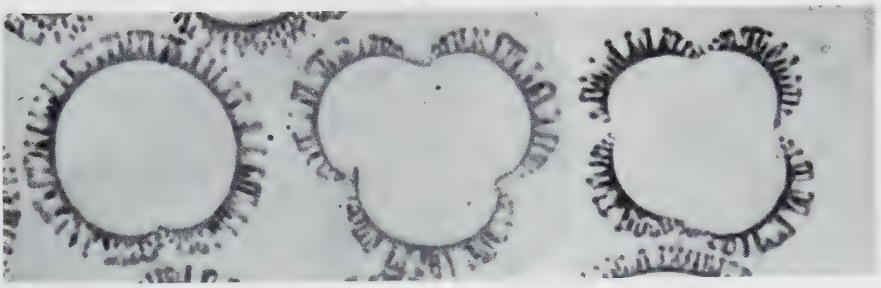

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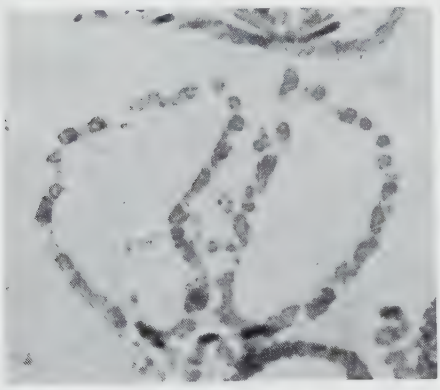

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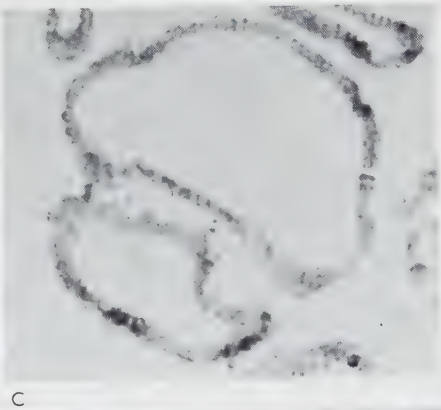

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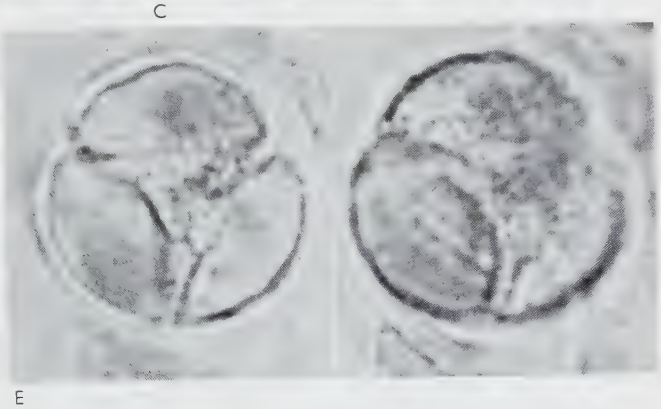

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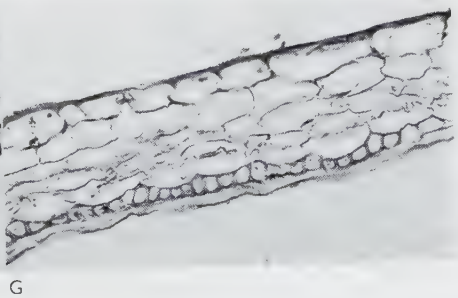

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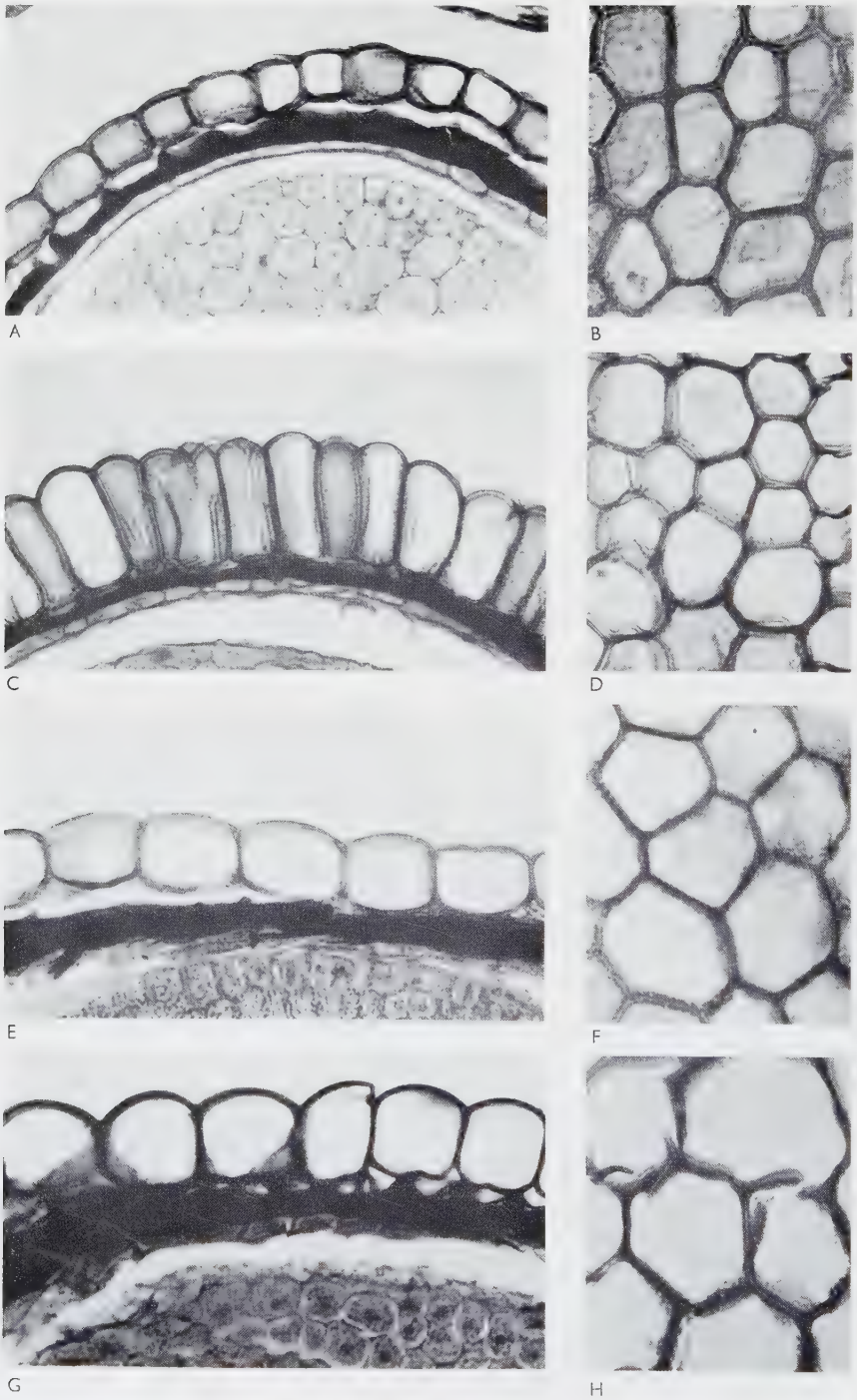
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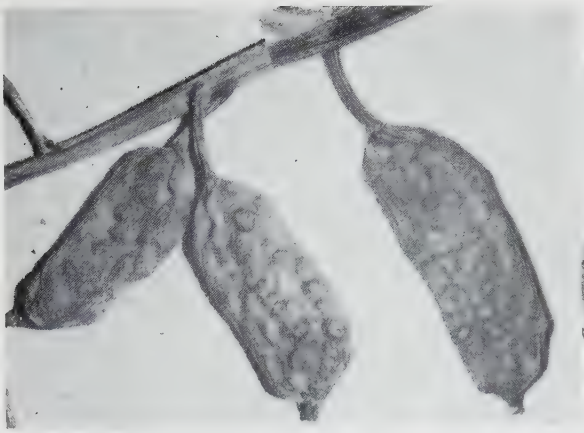

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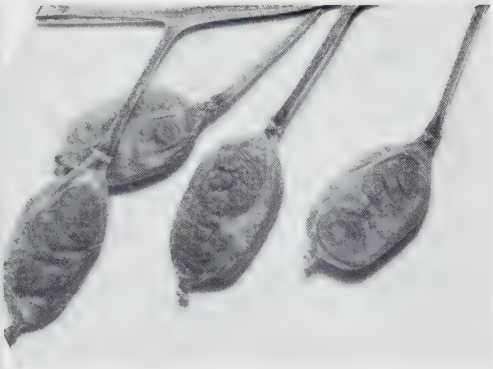

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